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Response of zooplankton to nutrient reduction and enhanced fish predation in a shallow eutrophic lake

Zhigang Mao[1] | Yong Cao[2] | Xiaohong Gu[1,3] | Qingfei Zeng[1] | Huihui Chen[1] | Erik Jeppesen[4,5,6,7]

[1]State Key Laboratory of Lake Science and Environment, Nanjing Institute of Geography and Limnology, Chinese Academy of Sciences, Nanjing, China

[2]Illinois Natural History Survey, Prairie Research Institute, University of Illinois, Champaign, Illinois, USA

[3]Huaiyin Normal University, Huaiyin, China

[4]Department of Bioscience, Aarhus University, Silkeborg, Denmark

[5]Sino-Danish Centre for Education and Research, Beijing, China

[6]Limnology Laboratory, Department of Biological Sciences and Centre for Ecosystem Research and Implementation, Middle East Technical University, Ankara, Turkey

[7]Institute of Marine Sciences, Middle East Technical University, Mersin, Turkey

Correspondence
Xiaohong Gu
Email: xhgu@niglas.ac.cn

Abstract

As a key link between top-down regulators and bottom-up factors, zooplankton responds sensitively to environmental variations and provides information on the ecological state of freshwater systems. Although the response of zooplankton to anthropogenic pressures and fluctuating natural conditions, such as nutrient loading and climate change, has been extensively examined, findings have varied markedly. The mechanistic basis for the correlation between environmental variability and the zooplankton community is still debated, particularly for subtropical eutrophic lakes. We used two methods to analyze physicochemical and selected biological variables derived from long-term monitoring of Lake Taihu, a subtropical shallow lake in China. We first applied random forest regression to examine how changes in zooplankton were related to a set of environmental variables on interannual time scales. Then we used the results to guide the construction of a conceptual model for piecewise structural equation modeling (pSEM) to quantify more precisely the zooplankton–environment relationship. Zooplanktivorous fish and nutrient concentrations were the most important predictors of long-term trends in zooplankton in RF regression. Intensification of planktivorous fish predation led to a lower zooplankton biomass and smaller individuals through the removal of larger crustaceans. Moreover, suppression of zooplankton can in part be explained by increases in inedible algae, triggered by a combination of reduced nutrient concentrations and weakened grazer control. These results were also confirmed in the pSEM, which further indicated that top-down regulators might be more important than bottom-up factors for the zooplankton community in Lake Taihu. Our results suggest that stocking of filter-feeding fish in the lake did not meet the expectation that they would control algae, but that the use of biomanipulation measures considering both water quality and fishery management seems promising. This study offers insights into how indicator metrics of zooplankton can improve our understanding of the associations between plankton communities and ecosystem alterations.

INTRODUCTION

Top-down effects can be just as important as bottom-up forces in structuring aquatic food webs (Carpenter et al., 1985). Changes at the top of the food web can trigger cascading effects through zooplankton to phytoplankton (Lemmens et al., 2018) and primary production (Cole et al., 2000), and even down to nutrient concentrations (Liu et al., 2018). Similarly, phytoplankton can also be regulated by nutrients and transfer energy to higher-trophic-level organisms through zooplankton. Thus, the zooplankton community is considered a vital component of the food web because of its sandwiched position between predators and primary producers. Moreover, researchers increasingly recognize that zooplankton is an important indicator of the structure and function of freshwater ecosystems and can provide information about the relative importance of top-down and bottom-up control (Haberman & Haldna, 2014; Vakkilainen et al., 2004). For example, a higher proportion of large zooplankton, larger cladoceran size, or increased zooplankton-to-phytoplankton biomass ratio generally indicates enhanced "top-down" control (Jeppesen et al., 2011). Similarly, a high zooplankton biomass or proportion of rotifers by numbers is closely linked with high "bottom-up" forces (Jeppesen et al., 2011).

The relative impacts of top-down and bottom-up forces on the zooplankton community can vary with environmental conditions (Jeppesen et al., 2003). Understanding the linkages between biological assemblages and their environment is thus crucial for the effective management and conservation of aquatic ecosystems. Indeed, there is a growing body of literature demonstrating the relationships between zooplankton communities and variations in natural and anthropogenic factors, including nutrient availability (Jeppesen et al., 2005), fish predation (Iglesias et al., 2011), aquatic plant refuge (Estlander et al., 2009), and climate change (Gyllström et al., 2005). For example, higher temperatures are associated with a shift in fish communities toward smaller sizes and higher densities due to enhanced and earlier reproduction as well as a faster growth rate and reduced longevity (Jeppesen et al., 2010). These changes may have strong, negative effects on zooplankton, through both increased planktivory and algal biomass (Lazzaro et al., 2003).

In recent decades, almost all types of freshwater systems have experienced eutrophication, typically resulting in a wide range of undesirable water quality changes and often massive cyanobacterial summer blooms (Smith et al., 2006). Extensive efforts have therefore been made across the globe to improve the ecological environment of many lakes and reservoirs by reducing external nutrient inputs (Huang et al., 2019; Jeppesen et al., 2005). However, although knowledge of the response of biological assemblages, especially phytoplankton, to reduced nutrient loading is extensive (Donald et al., 2011; Mao et al., 2020), much less is known about how the zooplankton communities change during this process. In the published literature on the response of zooplankton to nutrient availability, the response pattern has varied markedly, from less pronounced effects (Jeppesen et al., 2005) to substantive changes in community structure (Gyllström et al., 2005). In addition, fish biomanipulation (e.g., manual removal of zooplanktivorous fish or promotion of an abundant piscivorous fish community) has also been widely applied in restoration management (Mehner et al., 2002; Søndergaard et al., 2008). The desired reduction of planktivory is generally followed by an increase in the density of large-bodied zooplankton (predominantly cladocerans and copepods) and results in an increased grazing pressure on phytoplankton and, ultimately, higher water clarity. However, several studies have shown that tropical or subtropical fish assemblages are usually dominated by small planktivorous and omnivorous fish due to the relatively weak top-down grazing control by predatory fish (Jeppesen et al., 2010; Meerhoff et al., 2012). Large-sized zooplankton may, therefore, be subject to higher fish predation in the subtropics than in the temperate zone (Iglesias et al., 2011). Moreover, despite the importance of zooplankton body size for the maintenance of the clear-water state, few investigations have evaluated the critical factors shaping the size structure of the zooplankton (Jeppesen et al., 2011).

Zooplankton community structure and biomass depend on seasonal succession in lakes and reservoirs (Jeppesen et al., 2005). For instance, cladoceran abundance often shows a major increase during late spring followed by reduced grazing pressure in summer due to predation or blooms of inedible cyanobacteria (Sommer et al., 2012). However, previous studies of the relationships between zooplankton and the environment and the cascading effects from fish have mostly focused on the summer season (Dupuis & Hann, 2009), whereas comparatively little attention has been paid to seasonal dynamics (Li et al., 2019).

Hence, with the aim of testing for the temporal zooplankton response (interannual and seasonal time scales) to biotic and abiotic variables, we investigated a shallow, subtropical, and eutrophic lake, Lake Taihu. Lake Taihu is the third largest freshwater lake in China, and it has experienced severe human-caused pressures since the 1990s as a result of the rapid growth of the human population around the lake (rapid increases in nutrient loading, dramatic changes in climate status, and overexploitation and manipulation of fish) (Zhang et al., 2016). Previous studies discussed the considerable changes in the environmental conditions of the lake over recent decades (Zhang et al., 2016), as well as in the biological community structure (Liu et al., 2011; Mao, Gu, Zeng, Zhou, Wang, et al., 2011). Furthermore, a massive stocking of filter-feeding fish (bighead carp *Hypophthalmichthys nobilis* and silver carp *Hypophthalmichthys molitrix*) has been used as a biomanipulation tool to suppress phytoplankton in Lake Taihu, assuming that silver and bighead carps can effectively graze large cyanobacterial species (Zhou et al., 2009). However, this biological restoration has seemingly not achieved the desired goal, and its potential impact on the zooplankton community and the size distribution of the zooplankton have rarely been explored (Yi et al., 2016). Finally, several published surveys of zooplankton in Lake Taihu analyzed zooplankton–environment relationships using a fairly comprehensive data set of water chemistry and temperature (Li et al., 2019; Zhou et al., 2020), but many aspects of the lake environment important to the zooplankton, such as variability in predator and phytoplankton communities, have been neglected. Thus, different parts of the aquatic food webs need to be included in future studies to improve our predictive ability.

In this study, we analyzed a 12-year data set derived from the long-term monitoring of Lake Taihu. To analyze the complex zooplankton–environment relationships, we applied two complementary methods, random forest (RF) regression (Breiman, 2001) and piecewise structural equation modeling (SEM) (Lefcheck, 2016), to examine how zooplankton was related to environmental variables and biotic assemblages. Our study aimed to assess (1) how zooplankton changed on annual and seasonal time scales, (2) which limnological variables could best explain the zooplankton community variation, (3) whether top-down regulation by fish was the key factor determining zooplankton community composition and size structure, and (4) which zooplankton metrics would be useful indicators of the structure and function of lake ecosystems.

METHODS

Study area

Lake Taihu is a shallow eutrophic lake ($30°55'40''$– $31°32'58''$ N and $119°52'32''$–$120°36'10''$ E) located in the Yangtze River Delta, one of the most industrialized and densely populated regions in China. The area of the lake is 2338 km^2, and it has a mean depth of 2.4 ± 0.1 m and a watershed area of 36,895 km^2. Since the 1990s, urban and agricultural development in the basin has resulted in dramatic increases in nutrient loading as well as accelerated eutrophication, characterized by rapid water quality deterioration and increasingly severe cyanobacterial blooms (*Microcystis* spp.) during the warm season (Liu et al., 2011). In addition, nutrient enrichment combined with a long history of overfishing has been blamed for fishery declines in the region (Mao, Gu, Zeng, Zhou, & Sun, 2011). Consequently, management efforts are being made to rebuild the fisheries of the lake. For instance, Lake Taihu has been stocked intensively with various native species (e.g., predatory carp (*Cultrichthys erythropterus* [Basilewsky, 1855]), black carp (*Mylopharyngodon piceus* [Richardson, 1846]), common carp (*Cyprinus carpio* [Linnaeus, 1758]), white amur bream (*Parabramis pekinensis* [Basilewsky, 1855])) since 2009 for fishery recovery and as a supplement to declining populations (Mao et al., 2020). In addition, massive stocking of filter-feeding fish (silver carp and bighead carp) has been used as a biomanipulation tool in the attempt to suppress phytoplankton in the lake (Zhou et al., 2009) but without the expected effects (Mao et al., 2020).

Data sources

Water quality and plankton community data

In this study, a long-term data set (2005–2016) gathered by the Taihu Laboratory for Lake Ecosystem Research (CERN TLLER) was used for modeling. Plankton community and water quality samples were taken monthly at eight sites (Figure 1) for 12 years. Lake surface wind speed (Wind Speed) was measured synchronously. The water samples were collected with a 2-m-long and a 10-cm-diameter plastic tube at each site. A range of physical and chemical variables were measured, including Secchi disk depth (Secchi), water temperature, pH, total nitrogen (TN), total phosphorus (TP), ammonium (NH_4^+), and dissolved organic carbon (DOC) using the method of Jin and Tu (1990). Zooplankton samples were collected by sieving 10-L water samples through a 64-μm plankton net
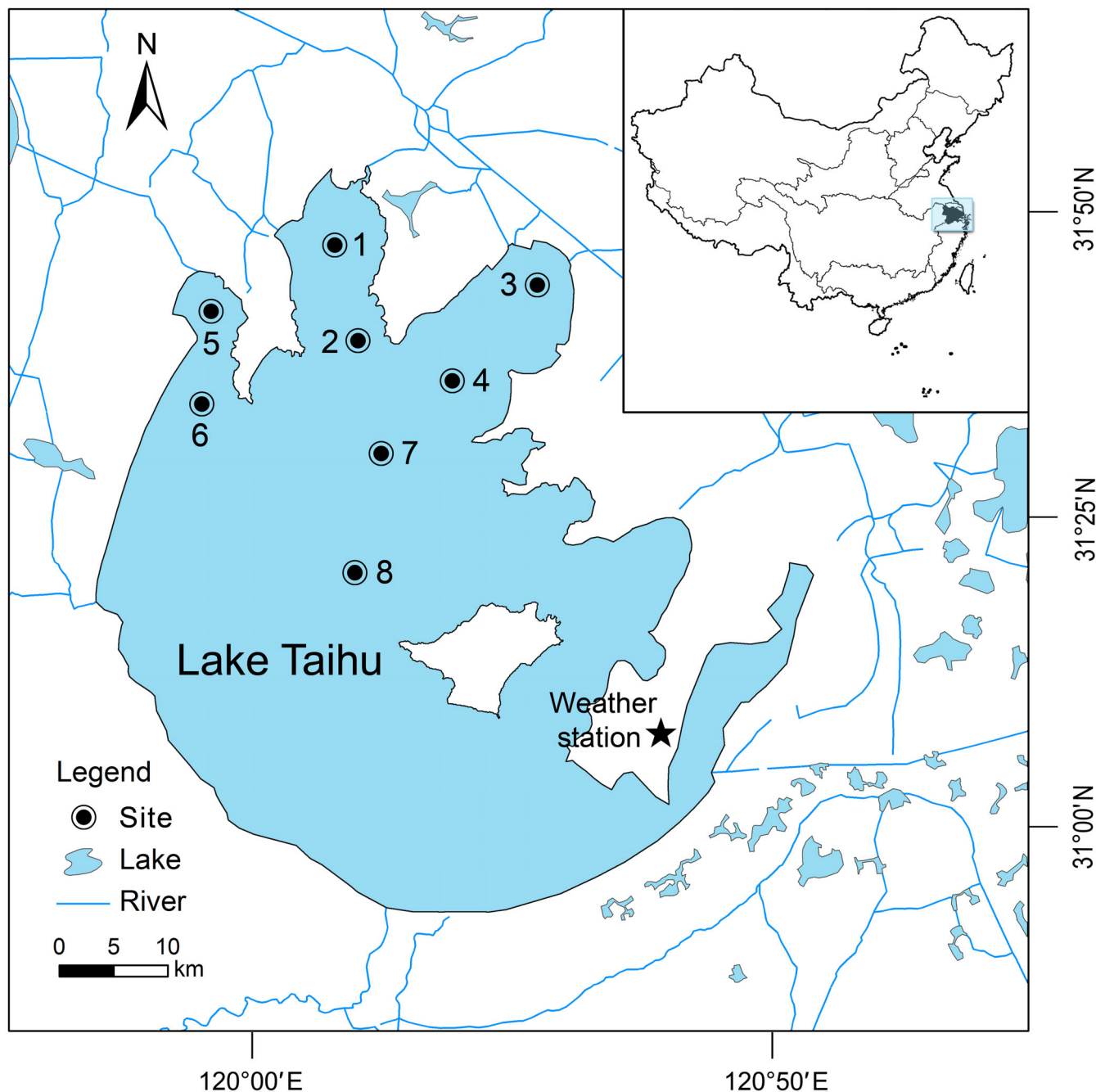
FIGURE 1 Locations of the eight sampling sites in Lake Taihu, China, 2005–2016.

and identified to the species or genus level (Chiang & Du, 1979). Individual body lengths were measured to calculate the wet weights of the zooplankton according to the weight-body size regression of Huang (1999). At least 20 individuals of each species were measured or all individuals if the total number was <20. Phytoplankton samples (500 ml) were fixed with Lugol's solution and sedimented for 48 h. Identification was made on species where possible and genus for the remaining species according to Hu and Wei (2006). Species volumes were estimated by assigning combinations of geometric shapes to fit the characteristics of individual taxa (Smayda, 1978).

Main cell dimensions were measured using an ocular micrometer for at least 30 randomly selected individuals. Total algal biovolume was calculated by the addition of the volume of all species present. The volume values were converted to biomass, assuming that 1 mm^3 volume was equivalent to 1 mg fresh weight biomass.

Fish community data

Fish data on Lake Taihu for the period 2005–2016 were obtained from the Lake Taihu Fishery Administration

Committee of Jiangsu Province. The data were compiled based on reports on commercial fishing operations submitted as part of a requirement for all licensed fishing vessels. The reports describe the location, duration, and fish catch (biomass of individual species) of the main commercial species, including lake anchovy (*Coilia ectenes taihuensis* [Yuen, Lin, Liu & Qin, 1977]), icefish (*Neosalanx tangkahkeii* [Wu, 1931]), silver carp, bighead carp, common carp, goldfish (*Carassius auratus* [Linnaeus, 1758]), and predatory carp (Appendix S1: Table S1). The commercial species comprised over 90% of the total lake fish catch (Mao, Gu, Zeng, Zhou, & Sun, 2011). The fish were assigned to different feeding groups: zooplanktivorous species (Zoop_Fish), benthivorous species (Ben_Fish) and piscivorous species (Pis_Fish) based on the literature (Li et al., 2009; Mao et al., 2012). Catch data were standardized by gear and duration prior to analyses, and catch per unit effort (CPUE) was calculated as kilograms per net per day (kg/net/day) (Appendix S1: Table S1, Figure S1).

Because we recognized the potential limitations of the commercial fishery data, we compared the commercial data with fish biomass estimates based on multimesh gillnet catches to check whether the rather coarse fishery data would be reliable for our analysis. In Lake Taihu, fish assemblages were sampled annually at six stations with multimesh gillnets during the 2012–2016 period. Sampling was conducted at the end of August to maximize the catch efficiency of the gillnets. At each station, two pelagic and two benthic gillnets (mesh sizes 5, 8, 13, 21, 29, 43, 60, and 80 mm) were deployed, covering the entire water column from the bottom to the surface. All nets were 100 m wide and 1.5 m deep and were set for 2 h. CPUE was calculated as kilogram of fish per gillnet per hour (Appendix S1: Table S2, Figure S1). We performed a Mantel test using the vegan package in R (Oksanen et al., 2014) to examine significant correlations in taxonomic composition (measured with the Bray-Curtis index) between the two data sets. Strong and significant correlations were found (Pearson $r = 0.8$, $p < 0.05$); thus, we concluded that the commercial fishery data could be used as an index of the sampling data for Lake Taihu.

Meteorological data

Monthly meteorological data from the Dongshan weather station (Figure 1) were used to evaluate the long-term climatic variations around the lake. Observational data from 2005 to 2016 were obtained from the China Meteorological Data Sharing Service System (http://cdc.cma.gov.cn/). The primary factors included temperature, annual solar radiation (Eg), and annual precipitation (AP).

Areas of aquatic vegetation cover from 2005 to 2016 in Lake Taihu were detected using satellite data (Luo et al., 2020). More details about the determination method are provided in Luo et al. (2020).

Data analysis

Environmental variables associated with natural and human-related lake characteristics were chosen a priori based on their demonstrated importance in shaping zooplankton communities in aquatic ecosystems. We gathered information on 17 environmental variables that describe natural conditions (e.g., water quality, climate, and habitat), biotic components (e.g., phytoplankton community and functional groups of the fish assemblage), and human activities (e.g., fish stock) in Lake Taihu (Table 1).

Temporal trends

We fitted the changes in zooplankton and environmental variables with generalized additive models (GAM) based on annual data (mean of monthly value across all sites) to show the long-term trend. All the variables (except for pH) were log-transformed [$\log_{10}(X + 1)$] to reduce distributional skewness. We also used correlation analysis to measure the strength or consistency of the long-term trend of zooplankton indices. As the temporal change of some variables was not linear, we calculated the Spearman rank correlation coefficient (ρ) with year.

Differences in zooplankton indices and environmental variables among the four seasons (Spring, Summer, Autumn, and Winter) were tested using one-way ANOVA with post hoc Tukey tests (e.g., TN) or, when a parametric test was not possible, the non-parametric Kruskal-Wallis test (e.g., zooplankton biomass) with a Bonferroni correction.

Random forest regression

Given that environmental variables often interact with one another in shaping biological assemblages in complex ways, the variance of biological responses explained by the individual environmental variables may strongly overlap, and the unique contributions of specific factors are difficult to quantify (Schwalb et al., 2013). As a result, we took two complementary approaches (RF regression and SEM) for our data analysis. Because our fish data were year-based estimations, it was not possible to consider the long-term trend of seasonality in the RF regression and SEM. Therefore, only the annual means of the variables were used in the two types of modeling.

TABLE 1 Description, mean, and range of 17 environmental and biological variables in Lake Taihu during 2005–2016.

Variables	Description	Mean	Median	SD	Max	Min
TP	Total phosphorus (mg/L)	0.14	0.13	0.02	0.16	0.12
TN	Total nitrogen (mg/L)	3.35	3.14	0.50	4.43	2.71
NH_4^+	Ammonium (mg/L)	0.73	0.75	0.22	1.07	0.29
DOC	Dissolved organic carbon (mg/L)	5.31	4.75	1.64	8.41	3.69
pH	Pondus hydrogenii	8.23	8.20	0.12	8.46	8.01
Secchi	Secchi depth (m)	0.39	0.38	0.04	0.45	0.33
Water temp	Water temperature (°C)	17.4	17.6	0.6	18.1	16.1
Eg	Annual solar radiation (MJ/m^2)	4755	4760	164	5014	4464
AP	Annual precipitation (mm)	1077	1011	245	1714	776
Wind speed	Lake surface wind speed (m/s)	3.05	3.18	0.45	3.60	2.17
Vegetation area	Aquatic vegetation cover area (km^2)	285	304	76	392	140
Phy_Biomass	Phytoplankton biomass (mg/L)	5.21	5.30	2.93	10.26	1.28
Cyano_Density	Cyanobacteria density (10^8 cells/L)	1.20	0.68	0.99	2.69	0.16
Zoo_Fish	Zooplanktivorous fish CPUE (kg net^{-1} day^{-1})	76.88	74.07	14.34	104.67	60.30
Pis_Fish	Piscivorous fish CPUE (kg^{-1} net^{-1} day^{-1})	0.76	0.72	0.36	1.38	0.25
Ben_Fish	Benthivorous fish CPUE (kg^{-1} net^{-1} day)	5.63	4.76	2.82	10.48	2.29
Fish stock	Fish stock biomass (t)	825	658	749	2664	166

RF regression is designed to accommodate different types of response curves and variable interactions (Breiman, 2001) and is a preferred tool to infer the impacts of major biotic assemblages and environmental variables on zooplankton components. RF regression also appears highly resistant to the effect of autocorrelation (Stuart-Smith et al., 2013), a legitimate concern because our environmental and biological data were collected over 12 consecutive years.

We used RF regression to model the effects of 17 environmental variables on the zooplankton community over time. In RF, the predictor variables were resampled to generate a large number of unpruned decision trees (5000 in our case). The relative contribution of a predictor variable to the model accuracy was evaluated based on how much the mean standard error (MSE) of the predictions increased when the values of this variable were randomized in the one-third of the samples used for testing. The more the MSE increased, the more important a variable was considered to be.

We built RF models for 12 response variables base on annual means of the predictors: (1) the biomass and density of zooplankton and each of three zooplankton taxonomic groups and (2) four metrics of the zooplankton community (i.e., mean individual body weight of zooplankton and cladocerans, the proportion of rotifers by numbers and zooplankton to phytoplankton biomass ratio [Zoop:Phyt ratio]). Multiple RF models were then structured for each response variable by progressively increasing the number of predictors used for group

splitting (i.e., mtry in the randomForest package in R) and rerunning the models five times at each level of mtry using different random seeds. The model with the highest R^2 for the out-of-bag samples (one-third samples not used for model calibration) was chosen as the final one. Of the 12 RF models, only those with $R^2 \geq 0.10$ were further investigated to identify which 10 predictors were most important. We then described the relationship between those predictors and the response index using partial-dependence plots (Cutler et al., 2007). The responses were classified into three types: positive, negative, and multimodal (V- or U-shaped or irregular).

However, RF regression as a black-box method is restricted in terms of quantifying the effects of environmental variables. Both MSE and the partial-dependence plot are diagnostic tools rather than estimations.

Piecewise structural equation modeling

Standard SEM has been commonly used to relate predictors to response variables in a causal network (Shipley, 2003). Piecewise SEM (pSEM) overcomes several restrictions of SEM (Lefcheck, 2016) and is now being increasingly adopted in ecological studies (Chevaux et al., 2022; Lázaro et al., 2020). Compared with standard SEM, pSEM offers an important advantage: Each path is fitted individually, so the requirement for sample size is reduced. More importantly, this feature allows one to use different families of

error distribution and account for autocorrelation (Lefcheck, 2016). We first developed a conceptual model for the response of zooplankton to top-down and bottom-up drivers in Lake Taihu based on the top predictors in the RF regression and our understanding of directional responses of the zooplankton communities to the predictors. Nine latent variables were used: nutrient concentrations (TN, NH_4^+, DOC), fish stock biomass, cyanobacteria density, zooplanktivorous fish CPUE, and the biomasses of small (rotifers) and large (copepods and cladocerans) zooplankton. Like Lefcheck (2016), we included a temporal correlation term in pSEM with the function corCAR1 from the nlme package to account for potential autocorrelation. We present the standardized coefficient for each path in the model. The model was built with the R package, piecewise SEM (version 2.1.2) in R version 4.0.3. The model performance is assessed with Fisher's C statistic, the standardized regression coefficients, and R^2 for individual paths.

RESULTS

Long-term dynamics of zooplankton community

Total zooplankton biomass generally decreased from 2005 to 2016, whereas zooplankton density did not display a strong temporal trend (Figure 2 and Appendix S1: Figure S2). These trends were also well indicated by the Spearman correlations ($n = 12$, $\rho = -0.81$ and $\rho = -0.12$, respectively). Consistent with this, the biomass of different taxonomic zooplankton groups showed similar decreasing trends ($n = 12$, $-0.85 \leq \rho \leq -0.43$), whereas none of their densities showed clear temporal trends ($n = 12$, $-0.39 \leq \rho \leq 0.15$) (Figure 2; Appendix S1: Figure S2). Densities were typically dominated by rotifers during the 12 years, and the biomass was dominated by cladocerans, particularly in the first half of the study period (Appendix S1: Figure S3).

All metrics of the zooplankton community, except the proportion of rotifers by numbers, varied strongly over time (Figure 2; Appendix S1: Figure S2). Zooplankton size decreased significantly after 2005 ($n = 12$, $\rho = -0.78$) (Figure 2d), whereas cladoceran size and the Zoop:Phyt ratio demonstrated significant decreasing trends until the middle of the study period ($n = 12$, $\rho = -0.90$ and $\rho = -0.87$, respectively; Figure 2e,f). Total phytoplankton biomass and density consistently increased over time, with high temporal correlation ($n = 12$, $\rho = 0.80$ and $\rho = 0.87$, respectively). By contrast, both TN and NH_4^+ concentrations continued to decrease ($n = 12$, $\rho = -0.80$ and $\rho = -0.87$), whereas TP concentrations largely remained stable ($n = 12$, $\rho = 0.01$) (Appendix S1: Figure S4).
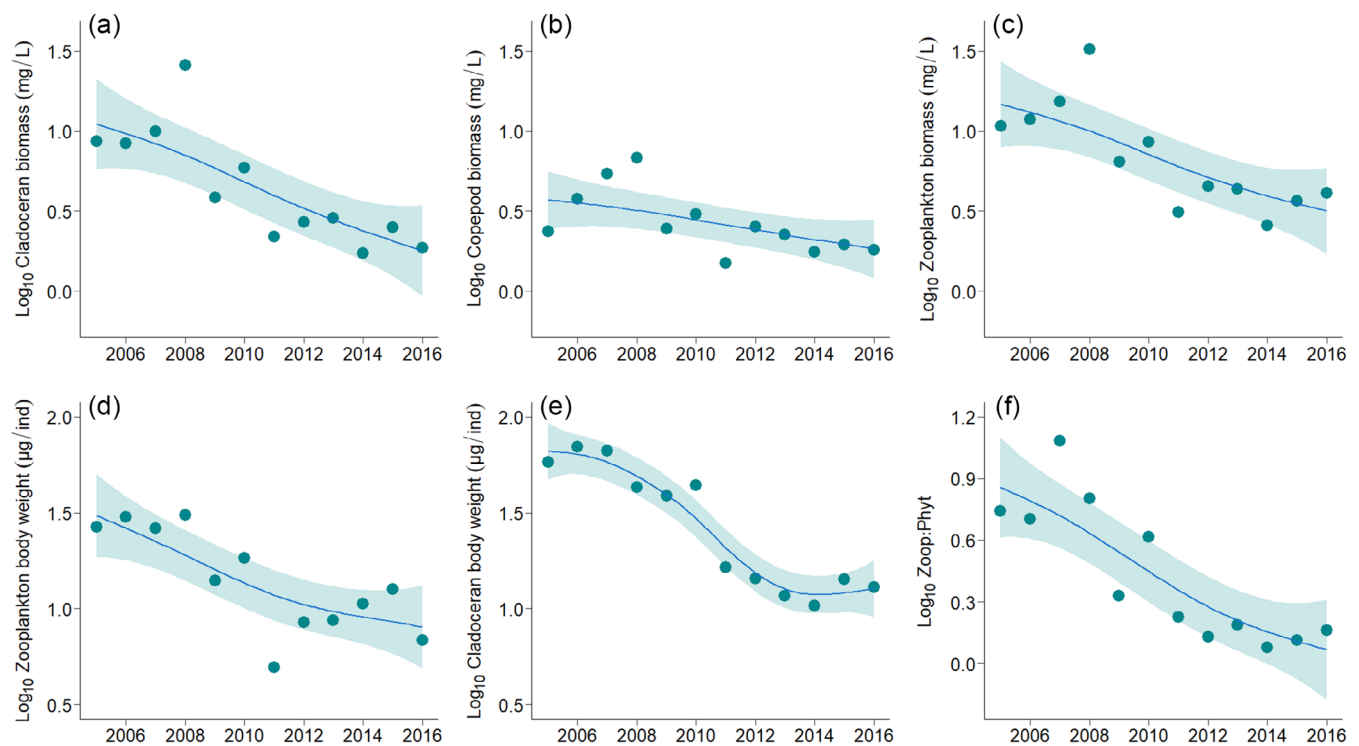

FIGURE 2   Long-term trends (generalized additive model) of annual biomass of (a) cladocerans, (b) copepods, and (c) zooplankton, mean individual body weight of (d) zooplankton and (e) cladocerans, and (f) zooplankton-to-phytoplankton biomass ratio (Zoop:Phyt).

Seasonal patterns of zooplankton community

Conspicuous seasonal changes were observed in the total biomass of zooplankton and cladocerans, both of which increased substantially in summer and autumn (Kruskal–Wallis, $n = 144$, $p < 0.05$; Figure 3a,b; Appendix S1: Figure S5). A clear seasonal pattern also occurred in the mean body weight of cladocerans: a spring peak followed by low values in summer and an increase again in winter (Figure 3c; Appendix S1: Figure S5). Phytoplankton biomass did not display a clear temporal trend (Kruskal-Wallis, $n = 144$, $p = 0.10$; Figure 3d; Appendix S1: Figure S6), but cyanobacteria density varied statistically significantly among seasons (Kruskal-Wallis, $n = 144$, $p < 0.05$; Figure 3e; Appendix S1: Figure S6).
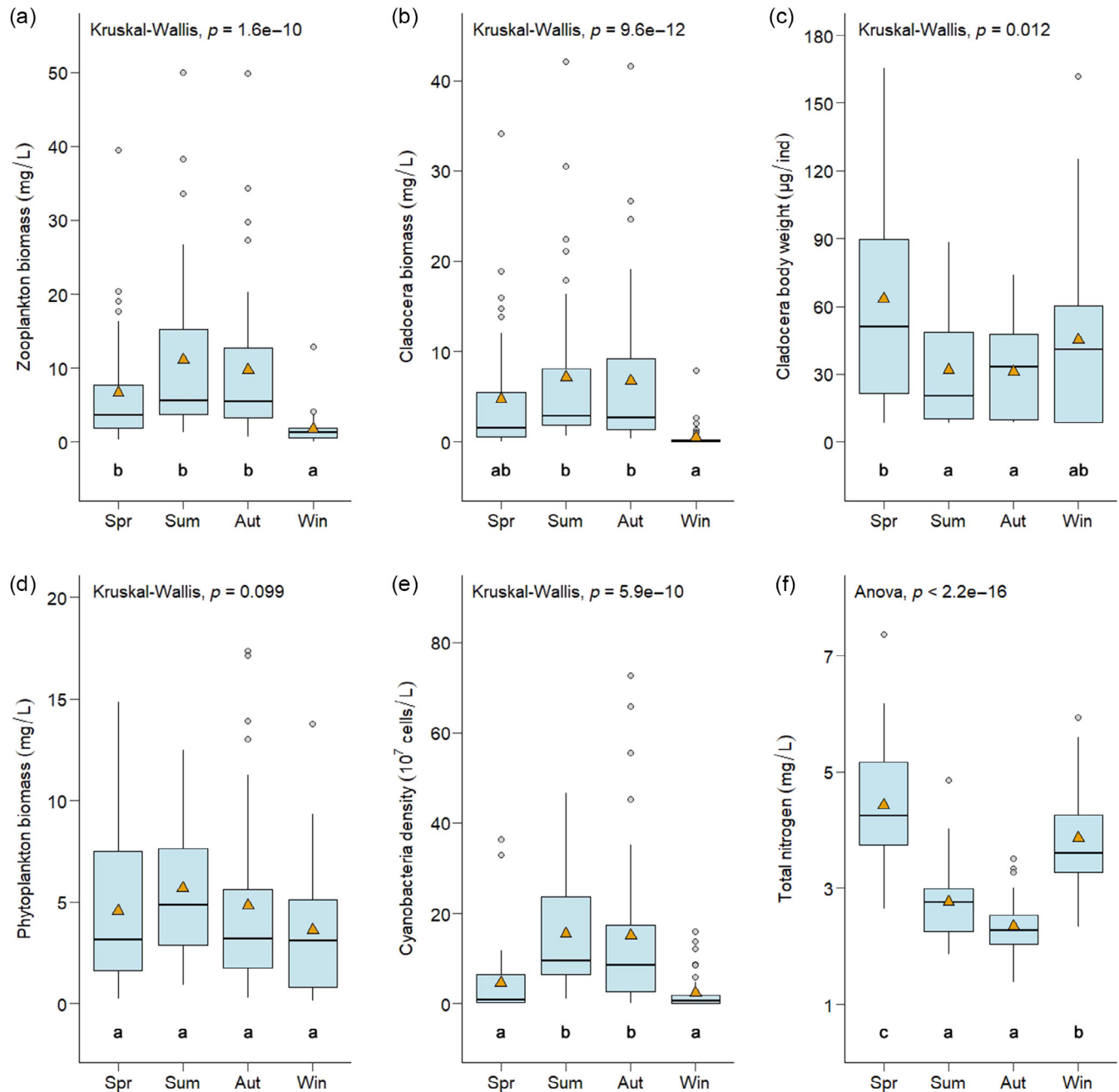
FIGURE 3 Seasonal variations in biomass of (a) zooplankton and (b) cladocerans, individual body weight of (c) cladocerans, (d) phytoplankton biomass, (e) cyanobacteria density, and (f) total nitrogen in Lake Taihu. Box plots: means (triangles), median (horizontal line in the middle of the box), interquartile range (box), and range (whiskers). Spr: spring (March–May); Sum: summer (June–August); Aut: autumn (September–November); Win: winter (December–February). Significant differences ($p \leq 0.05$) in zooplankton resources and environmental factors are indicated by different letters between the four seasons.

Cyanobacteria abundance showed an increasing trend during the warmer season, especially in summer. In contrast, TN was lowest during the warm season and highest during the cold season (ANOVA, $n = 144$, $p < 0.05$; Figure 3f; Appendix S1: Figure S6).

Environmental factors driving zooplankton resources

RF models were built for 12 response variables, with three to seven variables used for each split (mtry = 3–7), but only six models were >10% (Table 2). The zooplankton density models generally had a poor fit, with no model attaining $R^2 > 10\%$, and three biomass models accounted for >10% of the total variance (R^2 values). In addition, three RF models developed for metrics of the zooplankton community also accounted for 45%–71% of the total variance. These results indicated that zooplankton biomass and community composition were more strongly related to environmental factors than to density. Hereafter, we focus on these better-explained indices.

Although the importance of environmental variables (percentage MSE increase) varied among the six indices, some variables were generally important (Figure 4; Appendix S1: Table S3). For example, all six models ranked Zoop_fish, TN, NH_4^+, and DOC among their top five most important predictors (Table 2). In contrast, others were important only for specific response variables. For example, Cyano_Density was only marginally important for the biomass models (8%–10% MSE increase) but strongly important for cladoceran size (32% MSE increase).

Partial-dependence plots offered some insight into how the zooplankton community responded to a given environmental variable. We evaluated the impacts of the top 10 predictors for the six zooplankton indices (Table 2; Appendix S1: Figures S7, S8). For example, cladoceran, copepod, and total zooplankton biomass were all related positively to TN (Figure 5a) but negatively to zooplanktivorous fish (Figure 5b) and fish stock (Figure 5c). Similarly, the individual body weight of cladocerans and zooplankton increased with NH_4^+ (Figure 5d) but decreased with zooplanktivorous fish (Figure 5e) and cyanobacteria density (Figure 5f).

The pSEM was further used to evaluate the direct and indirect impacts of human activities and natural environmental variables on the zooplankton community. The nine most important predictors from the RF models were retained because we wanted to compare the relative contribution of top-down and bottom-up control on the zooplankton. Our pSEM fit the data well (Fisher's C = 27.01, AIC_c = 77.01, $p = 0.409$), with the conditional R^2 ranging from 0.91 to 0.99 (marginal R^2 = 0.28–0.90). The model revealed that cyanobacteria density was negatively influenced by NH_4^+ and DOC while being positively correlated to TN (Figure 6). Meanwhile, the bottom-up influence of cyanobacteria on large zooplankton was positive, but it had a strong negative

TABLE 2 Summary of top 10 predictors in random forests models and number of predictors with highest rank ≤3.

| Variables	Zooplankton biomass	Cladoceran biomass	Copepod biomass	Zooplankton size	Cladoceran size	Zoop:Phyt	Total (rank ≤ 3)
Pseudo-R^2	17.0	11.6	18.7	64.0	70.7	45.3	...
Zoop_fish	1 (−)	1 (−)	1 (−)	1 (−)	2 (−)	2 (−)	6
TN	3 (+)	2 (+)	3 (+)	2 (+)	4 (+)	1 (+)	5
Fish stock	2 (−)	3 (−)	5 (−)	3 (−)	8 (−)	4 (−)	3
NH_4^+	4 (+)	4 (+)	2 (+)	5 (+)	3 (+)	5 (+)	2
DOC	5 (+)	5 (+)	4 (+)	4 (+)	5 (+)	3 (+)	1
Cyano_Density	7 (−)	7 (−)	8 (−)	6 (−)	1 (−)	6 (−)	1
Pis_Fish	6 (−)	6 (−)	7 (−)	7 (−)	10 (−)	7 (−)	0
Eg	8 (+)	8 (+)	6 (+)	−	−	10 (+)	0
Ben_Fish	10 (−)	9 (−)	−	8 (−)	6 (~)	9 (−)	0
Phy_Biomass	−	−	−	10 (−)	7 (−)	8 (−)	0
Water temp	9 (+)	−	9 (+)	−	−	−	0
pH	−	−	10 (−)	9 (−)	9 (−)	−	0
Wind speed	−	10 (+)	−	−	−	−	0

Note: The effect of a predictor is labeled with + (positive), − (negative), or ~ (bimodal) (see Table 1 for full description of predictor variables).
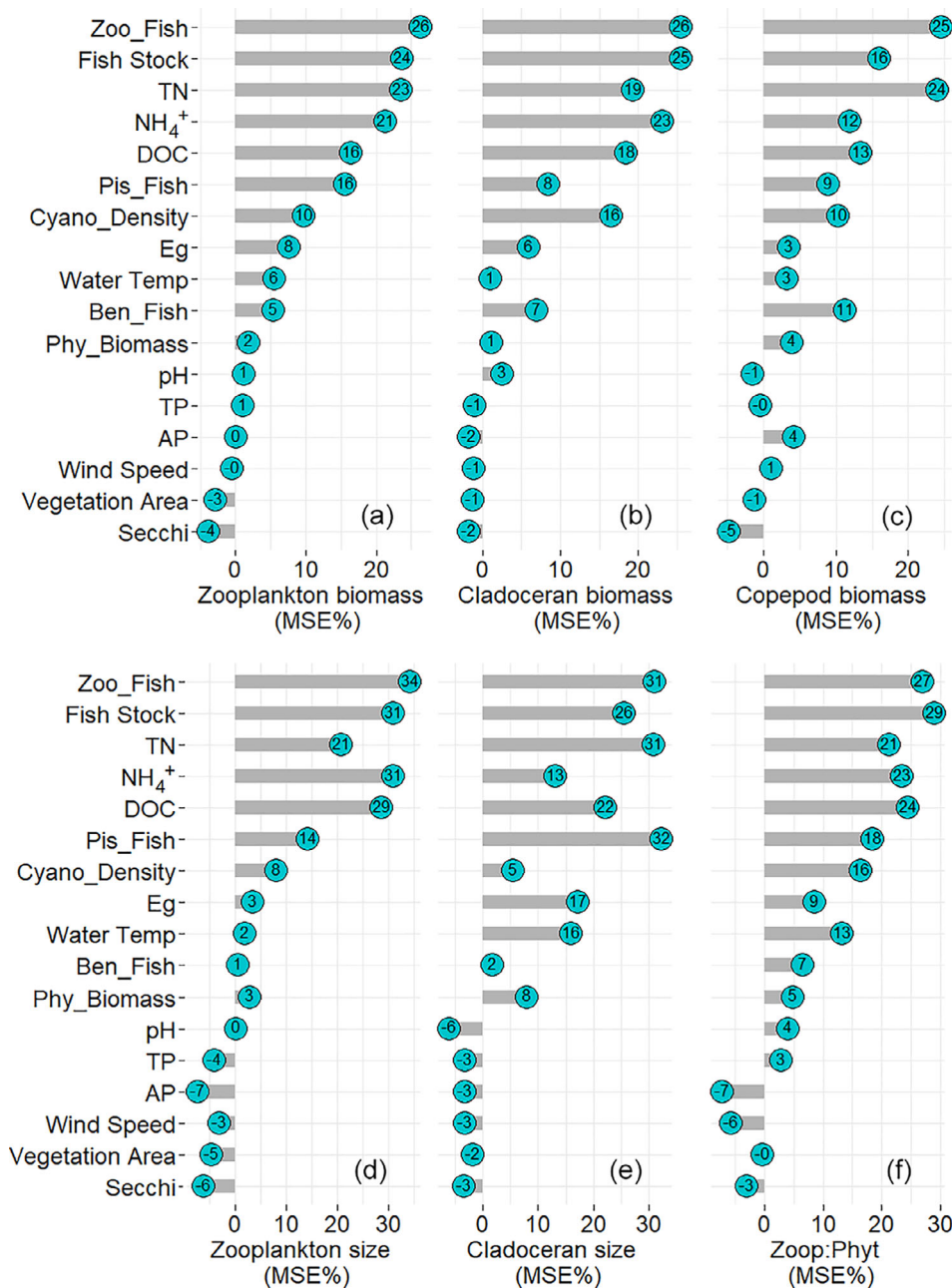
FIGURE 4 Importance values (percentage increase in mean standard error [MSE]) of the 17 environmental variables for predicting biomass of (a) zooplankton, (b) cladocerans, and (c) copepods; mean individual body weight of (d) zooplankton and (e) cladocerans; and (f) zooplankton-to-phytoplankton biomass ratio (Zoop:Phyt). Numbers in green circles are values of percentage MSE increase. AP, annual precipitation; Ben_Fish, benthivorous fish catch per unit effort; CPUE, catch per unit effort; Cyano_Density, cyanobacteria density; DOC, dissolved organic carbon; Eg, annual solar radiation; Fish Stock, fish stock biomass; NH_4^+, ammonium; pH, *Pondus hydrogenii*; Phy_Biomass, phytoplankton biomass; Pis_Fish, piscivorous fish catch per unit effort; Secchi, secchi depth; TN, total nitrogen; TP, total phosphorus; Vegetation Area, aquatic vegetation cover area; Water Temp, water temperature; Wind Speed, lake surface wind speed; Zoo_Fish, Zooplanktivorous fish CPUE.

effect on small zooplankton biomass, although neither is significant at the 0.05 level. We also observed that fish stocking activities increased the biomass of zooplanktivorous fish, indirectly suppressing the biomass of large-bodied zooplankton. Results from pSEM showed that the zooplanktivorous fish negatively

and significantly affected the large-bodied zooplankton but positively and insignificantly associated with small-bodied zooplankton. In summary, zooplankton biomass and community structure responded strongly to both nutrient reduction and fish predation in Lake Taihu (Figure 6).
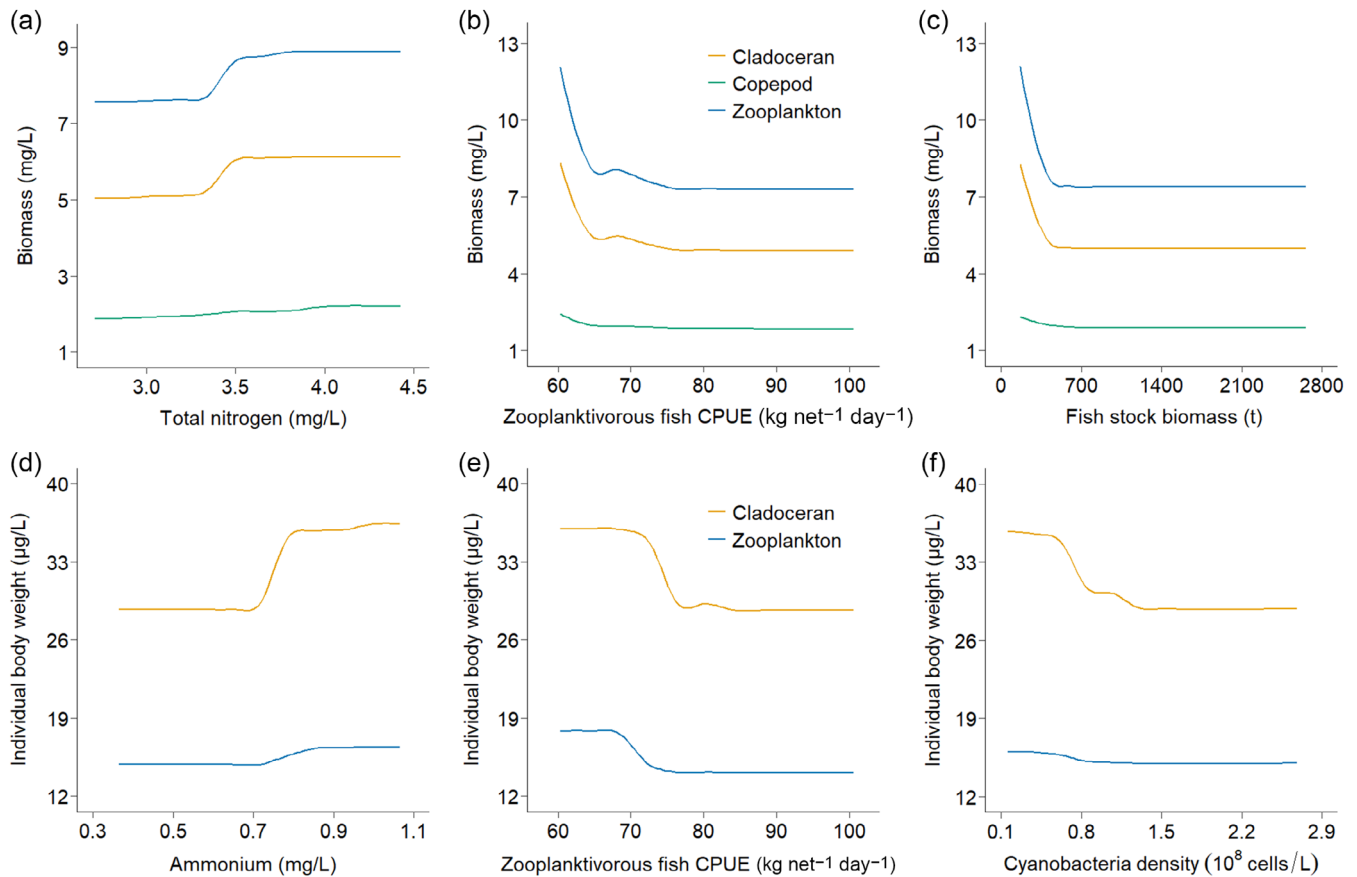
FIGURE 5 Examples of partial-dependence plots based on random forests regression showing responses of zooplankton biomass and individual body weight to key predictors: (a) total nitrogen, (b) zooplanktivorous fish, (c) fish stock, (d) ammonium, (e) zooplanktivorous fish, (f) and cyanobacteria density. CPUE, catch per unit effort.

DISCUSSION

We found that the long-term dynamics of the zooplankton community in Lake Taihu were closely related to nutrient loading and to fish predation pressure. Lower zooplankton biomass and smaller individuals occurred following decreased nutrient concentration and increased planktivorous fish abundance. The patterns of association between zooplankton and environmental variations indicated that the top-down regulators might be more important than bottom-up factors for the zooplankton community in the lake. These results offered new insights into the response of zooplankton to ecological processes and provided the information needed for the management of the lake.

Nutrient loading and fish predation shaping zooplankton communities

Given the strong, negative responses (e.g., undesirable water quality changes and severe cyanobacterial summer blooms)

to excessive nutrient loading in many freshwater systems, ecologists have been studying and managing eutrophied rivers and lakes in recent decades (Schindler, 1974; Smith et al., 2006). The response of zooplankton communities to nutrient gradients has also been examined extensively (Barbiero et al., 2009; Gyllström et al., 2005). According to most studies, a decline in the total biomass of zooplankton with decreasing nutrient concentrations is expected (Jeppesen et al., 2005). An explanation of this observed change in zooplankton is that a reduction in food availability, through continued reductions in nutrient loadings to water bodies, has exerted bottom-up controls on crustacean communities. For instance, a sharp decrease in phytoplankton production occurred against the backdrop of declining nutrient levels in Lake Huron during 2003–2006, which lends support to the suggestion that a declining food supply is a contributory factor to zooplankton biomass losses (Barbiero et al., 2009; Jeppesen et al., 2011).

We found that the zooplankton biomass in Lake Taihu also decreased significantly with decreasing TN and NH_4^+ (Figure 5; Appendix S1: Figure S4). However, this decline in zooplankton biomass was seemingly not
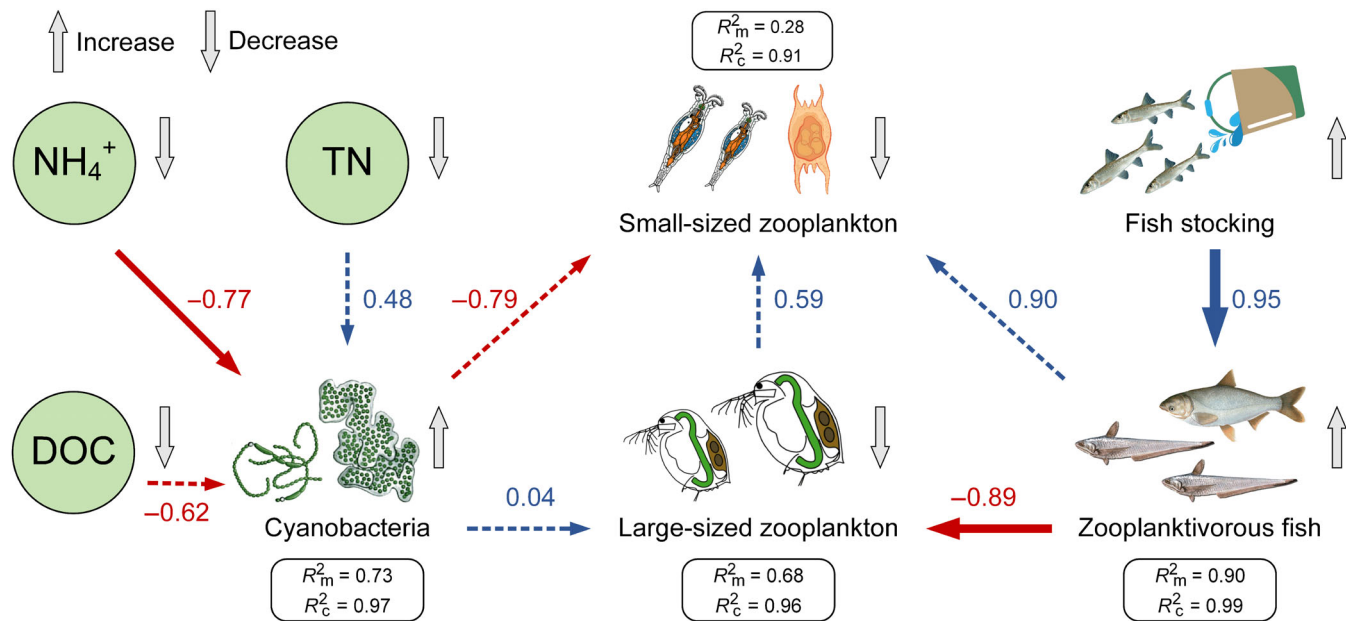
FIGURE 6 Conceptualized response of zooplankton to nutrient reduction and enhanced fish predation in Lake Taihu as estimated using piecewise structural equation modeling (pSEM). Gray hollow arrows indicate decreases or increases in biomass or concentration. Blue arrows denote positive relationships, red arrows negatives ones. Solid and dashed arrows respectively represent significant ($p \leq 0.05$) and nonsignificant effects. The thicknesses of the significant paths reflect the magnitude of the standardized regression coefficients given alongside. Marginal (R^2_m) and conditional (R^2_c) R^2 for component models are given in the boxes next to the response variables. DOC, dissolved organic carbon; NH_4^+, ammonium; TN, total nitrogen.

provoked by the mechanism described earlier (i.e., the reduction of phytoplankton production limits the food supply of zooplankton) because the total phytoplankton biomass increased over the study period. Although less common, negative relationships between zooplankton biomass and phytoplankton biomass were also found in other nutrient-rich lakes, which has been attributed to N subsidy-stress effects (Filstrup et al., 2018; Mao et al., 2020). Yoshiyama and Sharp (2006) summarized decades of data from the Delaware Bay and observed that Chl*a* decreased at high nutrient concentrations and accordingly classified these systems as "High-Nutrient, Low-Growth" systems. However, another, and perhaps more likely explanation of the suppression of zooplankton, is an increase in the share of inedible algae (e.g., filamentous or colonial cyanobacteria), which are generally considered too large to be edible by zooplankton (McCauley et al., 1999). Consistent with this view, in our investigation cyanobacteria consistently increased from 2005 to 2016 (Appendix S1: Figure S4). The pSEM model also showed that the cyanobacteria density had a negative effect on small-sized zooplankton biomass, although not to a significant level ($p = 0.15$) (Figure 6). Suppression of zooplankton in other systems, such as Lake Washington (Washington, D.C., USA; Hampton et al., 2006), has also been attributed to increases in inedible algae.

Several studies found that zooplankton can control phytoplankton when large crustaceans are not removed by fish (Vakkilainen et al., 2004). In a biomanipulation, major changes occurred in the phytoplankton composition following fish kills, and especially the biomass of nuisance cyanobacteria was notably reduced (Søndergaard et al., 2008). However, if large grazers are subject to high-intensity predation, the grazer control of phytoplankton would weaken (Power, 1992). Our results support the latter as our analyses indicate that fish markedly reduced the biomasses and individual size of large grazers in Lake Taihu (Figure 2), and the remaining small grazers likely were unable to suppress phytoplankton. Moreover, the Zoop: Phyt ratio also decreased during the monitoring period, indicating enhanced top-down control on zooplankton and reduced grazing on phytoplankton (Jeppesen et al., 2011). Sandwiched between phytoplankton and fish, zooplankton respond not only to food limitation but also to the predation pressure.

Our RF model indicated that the changes in both zooplankton biomass and size were best explained by the CPUE of zooplanktivorous fish, which showed a clear increasing trend during the study period (Appendix S1: Figure S1). The pSEM model also revealed that the zooplanktivorous fish negatively and significantly affected the large-bodied zooplankton (Figure 6). Thus, an intensified planktivore predation pressure

most likely caused the decline of large crustaceans. Both RF regression and pSEM support the explanation. Additionally, overfishing of apex predators in Lake Taihu may have created conditions favorable for small zooplanktivorous fish, especially lake anchovy, which accounts for almost 50% of the total annual catch in the lake (Appendix S1: Table S1; Mao et al., 2020).

Furthermore, predation effects were not only evidenced by the lower biomass of large-bodied zooplankton in Lake Taihu but also by their lower mean body sizes. The individual body weight of cladocerans demonstrated a significant decreasing trend after 2008, coinciding with the marked increase in the stocking and biomass of planktivorous fish (Appendix S1: Figure S1). Post-2008, higher intensive stocking (a mean annual stocking over 1000 tons) with a variety of species has been conducted in Lake Taihu for fisheries recovery (Appendix S1: Table S1; Gu et al., 2019). Meanwhile, a massive stocking of filter-feeding fish (mainly bighead carp) has been used as a biomanipulation tool in the attempt to suppress phytoplankton in the lake (Zhou et al., 2009). Most planktivores are size-selective, preferentially consuming the largest available individuals and thereby shifting the size structure of zooplankton toward smaller taxa (Jeppesen et al., 2004). Changes in the dominant species of zooplankton also supported this trend. Zhou et al. (2020) noted that the cladocerans in Lake Taihu were dominated by *Ceriodaphnia cornuta*, *Moina macrocopa* and *Bosmina coregoni* during 2007–2018, with the small cladocerans *Bosmina coregoni* dramatically increasing in the second half of the study period. Moreover, among the copepods, a major shift occurred from the dominance of large copepod species *Sinocalanus dorrii* and *Mesocyclops leuckarti* to small-sized *Limnoithona sinensis* (Zhou et al., 2020).

Last, the seasonal dynamics of zooplankton in Lake Taihu generally followed the pattern of the long-term variation described above, that is, zooplankton biomass and individual size were shaped by both nutrient loading and fish predation. For instance, total phytoplankton and cyanobacteria increased particularly in summer at reduced TN and NH_4^+ concentrations, indicating that nutrient constraints played an important role in determining seasonal responses. Another explanation for this relationship might be that the increase in cyanobacteria caused increased nutrient uptake and, therefore lower inorganic nutrient concentrations (O'Neil et al., 2012). Furthermore, a decline in the size of cladocerans during summer was observed in the lake, which is often ascribed to increased predation by fish (Brooks & Dodson, 1965). A similar shift has been found in several other lakes, for instance, in the Mediterranean region (Romo et al., 2005), where large-bodied zooplankton was abundant in early spring with few fish, while small-sized

zooplankton dominated when fish were abundant. Although the dominance of small forms in summer might be due to the direct effect of temperature on metabolism and physiological constraints (Gillooly & Dodson, 2000), it also coincides with the time when the dominant fish species (e.g., lake anchovy) reproduce and recruit high numbers of young-of-the-year planktivores (Mao, Gu, Zeng, Zhou, Wang, et al., 2011). These young fish prey exclusively on zooplankton and would have begun exploiting larger cladocerans by the time of early summer (Barbiero et al., 2009).

However, the long-term seasonal dynamics of the cladocerans showed that the above trend gradually weakened with the year-round fish stocking. In 2009, over 700 tons of fish were stocked in the lake from the beginning of spring, and stocking with a variety of species has continued at regular intervals ever since. After that, the spring peak of cladocerans has progressively disappeared, and their biomass and individual body weight have significantly decreased. Last, unlike the interannual variation pattern, the biomass of zooplankton and cladocerans during the warmer season did not decrease with nutrient reduction and enhanced fish predation. Faster reproductive rates of crustaceans could support the observed increasing trends through the system (Rozon et al., 2018). Consistent with this explanation, densities of copepods and cladocerans were significantly higher during the warmer season (Appendix S1: Figure S5b).

Implications for monitoring and biomanipulation of lake ecosystems

Cascading effects have long been predicted by theory and supported by empirical studies (Carpenter et al., 1985; Lemmens et al., 2018), and they represent one of the most important findings from our analyses. At higher trophic levels, changes in pelagic planktivore populations can influence the extent of competition and energy routing through food web pathways (Carpenter et al., 2001). This study has shown that the enhanced zooplanktivorous fish predation in Lake Taihu, triggered by a combination of fish overexploitation and stocking, may negatively affect the resilience of the lake by decreasing the density of large-sized zooplankton and thus the top-down control on phytoplankton (Iglesias et al., 2011; Mao et al., 2020). Also, the stocking of filter-feeding fish in the lake did not meet the expectations of algae control but had the opposite effect. Therefore, in light of this work, it is essential to ensure that fisheries managers are aware that fish are only one component of limnetic food webs. Fisheries management is being

shifted from individual focal species to the ecosystem-based approach and serving multiple goals, including biodiversity conservation, so we need to better understand how management practices influence food-web and ecosystem processes (Eby et al., 2006).

Most studies of food web manipulations confirm that biomanipulation is an effective and powerful tool for water quality improvement and freshwater ecosystem restoration when coupled with adaptive holistic management strategies (Mehner et al., 2002; Søndergaard et al., 2008). The results obtained in this study and other biomanipulation experiments can serve as the basis for designing appropriate fish manipulation measures and for predicting the success of future biomanipulation. First, fishery activities targeting planktivory can be applied to control the rise of mesopredators in the restoration of limnetic ecosystems (Jeppesen et al., 2011). For several species (e.g., lake anchovy) in Lake Taihu, commercial fishing may be an option. Second, the desired reduction of planktivorous fish may also be achieved by promoting the abundance of piscivorous fish through protection and stocking in order to increase the predation pressure on the planktivores (Eriksson et al., 2009; Potthoff et al., 2008). However, the overall effect may be moderate, given that piscivory is modest in warm lakes (Meerhoff et al., 2012). Third, our results indicate that heavy stocking of filter-feeding fish in Lake Taihu is not a suitable fish manipulation measure to control phytoplankton, and use of this strategy should therefore be immediately ceased. The combination of water quality management and fisheries management appears to be a particularly promising manipulation tool.

Zooplankton occupies an important and strategic position within aquatic food webs and are sensitive to environmental variation and may, therefore, be an important indicator of changes in trophic dynamics and ecological conditions (Vakkilainen et al., 2004). In this article, we built 12 RF models to assess whether and which zooplankton metrics could be useful indicators of the structure and function of lake ecosystems. Our results suggested that six metrics representing the biomass and size of zooplankton were strongly related to environmental factors. Similar to the examples of Danish lakes (Jeppesen et al., 2011), the zooplankton biomass in Lake Taihu indicated "bottom-up" processes, while zooplankton size, cladoceran size, and the Zoop:Phyt ratio mainly pointed to the importance of "top-down" processes. In addition, cladoceran size appeared as the most promising indicator to assess ecological change induced by environmental variations and/or human disturbances since the RF model developed for it accounted for a much higher total variance than the other models. Cladoceran assemblages could respond sensitively to variations in predation pressure, resource provision, and habitat availability due to their central position in the food web (Jeppesen et al., 2011). Thus, a combination of "top-down" and "bottom-up" indicator metrics would, of course, provide a complete assessment of the trophic conditions of lakes.

Finally, while our monitoring data set provides a comprehensive picture of water quality, climatic features, biotic assemblages, and different taxonomic zooplankton groups, information on zooplankton species composition and richness was not included. However, the community data derived at the species level can offer more insights into the changes in zooplankton communities, such as which dominant species drive changes in zooplankton biomass and size distribution (Jeppesen et al., 2011). Besides, certain zooplankton species show high sensitivity to environmental degradation and thus can be used for monitoring and assessment of lake biological conditions (Anas et al., 2013; Lougheed & Chow-Fraser, 2002). Therefore, providing species-level information in future long-term monitoring of Lake Taihu can be beneficial not only for a deeper understanding of zooplankton community dynamics but also for improving our predictive capacity.

CONCLUSIONS

Our results suggest that the interannual and seasonal dynamics of the zooplankton community responded not only to increased resource control but also to enhanced consumer control. Intensified zooplanktivorous fish predation appears to decrease zooplankton biomass and individual size due to the removal of larger-sized crustaceans. Moreover, the suppression of zooplankton may be explained by increases in inedible algae, triggered by a combination of reduced nutrient concentrations and weakened grazer control. Our analyses also raise concern about the certain biomanipulation in freshwater ecosystem restoration. We propose that heavy stocking of filter-feeding fish in Lake Taihu is not effective to control the phytoplankton, however, commercial fishing targeting planktivory and protection and stocking measures to increase predation pressure could be more beneficial adaptive management strategies. Planktivory-species stocking has been clearly identified to be one of the reasons for the observed lack of response to nutrient loading reduction (Qin et al., 2019) and has done more harm than good. Last, our data indicate that both "top-down" and "bottom-up" indicator metrics respond sensitively to environmental variations; thus, complementary use of these indicators may yield a more solid assessment of ecological conditions and functional changes in freshwater ecosystems.

CONFLICT OF INTEREST
The authors have no conflicts of interest.

DATA AVAILABILITY STATEMENT
Water quality and plankton community data are sensitive and not available publicly; these data are owned by the Nanjing Institute of Geography and Limnology, Chinese Academy of Sciences and they may be contacted for access. Fish community data (Mao, 2022) are available from Open Science Framework at https://doi.org/10.17605/OSF.IO/M38A5.

ORCID
Yong Cao https://orcid.org/0000-0002-1732-6491
Xiaohong Gu https://orcid.org/0000-0002-7635-5866

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.