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Abiotic and biotic drivers of temporal dynamics in the spatial heterogeneity of zooplankton communities across lakes in recovery from eutrophication

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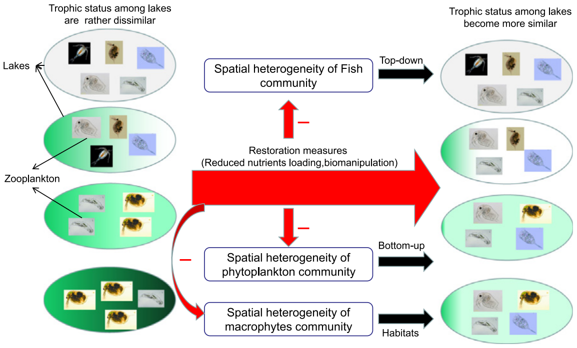
HIGHLIGHTS

- Temporal trends in spatial zooplankton heterogeneity across lakes are quantified.
- Heterogeneity of zooplankton exhibits strong seasonality.
- Spatial turnover dominate the temporal dynamic of zooplankton beta diversity.
- Restoration measures cause spatial homogenisation of macrophyte, fish and plankton.
- Bottom-up, top-down forces and macrophytes drive spatial zooplankton heterogeneity.

GRAPHICAL ABSTRACT



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ABSTRACT

Seasonal and annual dynamics of the zooplankton community in lakes are affected by changes in abiotic drivers, trophic interactions (e.g., changes in phytoplankton and fish communities and abundances) and habitat characteristics (e.g. macrophyte abundance and composition). However, little is known about the temporal responses of the zooplankton community to abiotic and biotic drivers across lakes at the regional scale. Using a comprehensive 20-year dataset from 20 Danish lakes in recovery from eutrophication, we assessed the seasonal and annual trends in the spatial heterogeneity of zooplankton community across lakes and related it to abiotic and biotic drivers. We found significant seasonality and inter-annual decreases in spatial zooplankton heterogeneity in both shallow and deep lakes, with the decrease in the spatial turnover dominating the temporal dynamics of the beta diversity. For the inter-annual changes, decreased spatial heterogeneity of phytoplankton, macrophytes and fish were important biotic drivers at the regional scale. Using a series of ordinary least squares regressions and model selection with model averaging approaches, we revealed that both local (e.g., total phosphorus, total nitrogen, pH, Secchi depth, alkalinity, Schmidt stability, water temperature) and regional drivers (e.g., air temperature, solar irradiance) were important variables influencing the spatial zooplankton heterogeneity, although the directions depended on the beta diversity measures and water depth. Our results highlight an

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important role of bottom-up forces through phytoplankton community as well as macrophytes and top-down forces via fishes in driving the temporal changes in zooplankton community composition patterns at the regional scale.

1. Introduction

Zooplankton have been widely suggested as an important indicator of the ecological status of lakes as they are affected by changes in both top-down and bottom-up control and may have a strong effect on water clarity (Carpenter et al., 2001; Jeppesen et al., 2011; Yuan and Pollard, 2018). The diversity and abundance of zooplankton are an indicator of water quality and trophic conditions in both cold, temperate and tropical waters (Barnett and Beisner, 2007; Lin et al., 2017; Jeppesen et al., 2000; Kuczyńska-Kippen and Joniak, 2016; Lopes et al., 2014). Thus, understanding how zooplankton community composition varies over space and time (i.e., beta diversity) has become a central topic in lake ecology and management (Liu et al., 2020; Loewen et al., 2019; Lopes et al., 2017; Soininen et al., 2007).

The temporal dynamics (e.g., seasonal and annual scale) of the zooplankton community result from changes in both abiotic (e.g., nutrients, light, temperature, pH, Schmidt stability etc.) and biotic drivers (e.g., primary production and predation) during either eutrophication or recovery from eutrophication in lake ecosystems (Ana and GeraldesMaria-José, 2007; David et al., 2020; Gyllstrom et al., 2005; Jeppesen et al., 2005a; Josué et al., 2018; Oliveira et al., 2020; Perera et al., 2021; Setubal and Riccardi, 2020; Xiong et al., 2017). For example, eutrophication often results in an increase in zooplankton biomass and a decrease in zooplankton species richness as well as marked changes in the zooplankton community composition, e.g., a decreased *Daphnia spp.*:total cladoceran biomass ratio and an increased cyclopoid:total copepod biomass ratio (Alta et al., 2017; He et al., 2020; Hsieh et al., 2011; Jeppesen et al., 2000). Conversely, recovery from eutrophication would expectedly lead to increases in zooplankton richness coupled with increases in the *Daphnia spp.*:cladoceran biomass ratio and the size of *Daphnia* species and other cladocerans (Dietmar and Walter, 1998; Jeppesen et al., 2005a; Jeppesen et al., 2005b). Notably, these modifications of the zooplankton communities subjected to changes in trophic status are generally a result of changes in the relative importance of alterations in resource control (bottom-up, e.g., phytoplankton) and predator control (top-down, e.g., planktivorous fish abundance) as well as changes in the coverage of macrophytes (He et al., 2018; Jeppesen et al., 1998b; Liu et al., 2014; Matsuzaki et al., 2018; Setubal and Riccardi, 2020; Yuan and Pollard, 2018). While a congruent pattern between phytoplankton and zooplankton has often been reported in temperate lakes during oligotrophication (Özkan et al., 2016), top-down controls from changes of fish community structure on zooplankton is highly dependent on water depth of lake (Jeppesen et al., 1997), but may not least in shallow lakes also be influenced by macrophyte coverage, providing refuges for certain zooplankton (Burks et al., 2006; Setubal and Riccardi, 2020). Previous studies have mainly been based on the temporal response of zooplankton communities to these abiotic and biotic drivers during eutrophication or recovery from eutrophication at the local scale (i.e., within lake) (Barnett and Beisner, 2007; Jeppesen et al., 2005a; Jeppesen et al., 1998a; Özkan et al., 2014). At the regional scale, however, the temporal changes in trophic status as well as local abiotic variables (e.g., total phosphorus, total nitrogen, pH, suspended solids, Secchi depth etc.) may differ across the landscape due to differential measures (e.g., reduction of external nutrient loading, biomanipulation) and efforts taken to protect or restore the ecosystems (Jeppesen et al., 2005b). Furthermore, regional abiotic variables (e.g., temperature, precipitation, etc.) could exhibit spatial heterogeneity across lakes in a given landscape (Beisner et al., 2006; Dallas and Drake, 2014; Heino et al., 2015). The spatial differences in local and regional driving forces may result in distinct trophic interactions among aquatic biotas with cascading effects (i.e., bottom-up and top-down control) on zooplankton communities (Beisner et al., 2006; Massicotte et al., 2014; Meier et al., 2015; Voelker and Swan, 2020). Therefore, while the spatial heterogeneity of zooplankton communities could potentially be an important indicator determining the ecological state of lakes across a landscape, the contribution of temporal changes in the abiotic (e.g., local and regional factors) and biotic drivers (e.g., phytoplankton, macrophytes and fish) to the spatial heterogeneity of zooplankton communities is not well understood.

In this study, we aimed at assessing the beta diversity of zooplankton communities across shallow and deep lakes in recovery from eutrophication. We examined the relative importance of regional (e.g., air temperature, precipitation, solar irradiance, wind speed etc.) and local abiotic drivers (e.g., water environments, considering factors such as N and P, chlorophyll *a*, pH, water temperature, suspended solids, Secchi depth etc.) in determining the long-term trends in spatial heterogeneity of zooplankton communities. Specifically, we were interested in assessing how the temporal trends in the spatial heterogeneity of zooplankton community were related to those in the spatial heterogeneity of phytoplankton, macrophytes and fish communities.

2. Materials and methods

2.1. Data collection

Twenty lakes were monitored between 1989 and 2008 as part of the Danish monitoring programme on the aquatic environment, NOVANA (Fig. S1). Lakes were sampled from March to November. The average sampling interval of the lakes was 14 days from May to October and 30 days in the other months. The total number of sampling days was 360 for each lake across the study period (1989–2008). Phytoplankton samples were taken mid-lake at depth-integrated locations covering the photic zone (i.e., 2*times the Secchi depth). Zooplankton densities were determined using depth-integrated water samples taken with a Limnos sampler (from the top to the bottom) from three mid-lakes stations and pooled. Details on plankton sampling, identification, counting, measurements of abiotic variables and data curation for lakes can be found in Özkan et al. (2014) and Fu et al. (2020). All plankton taxa were aggregated to genus level (Özkan et al., 2014). For the macrophyte data, we calculated the PVI index as percentage of plant volume infested using plant coverage and plant height for each year in combination with water depth from 1993 to 2007. For the fish data, we calculated the catch per unit effort of fish in terms of biomass and number (i.e., piscivores and planktivores) in the lakes using standardised gillnet fishing. Details on macrophyte sampling methods are available in Özkan et al. (2014) and on fish in Jeppesen et al. (2005a). The sampling frequencies of macrophytes and fish of all lakes included in this study are shown in Table S1 as they differed from the more regular sampling of abiotic variables, phytoplankton and zooplankton.

The local abiotic variables including Schmidt stability index for the deep lakes only (an index of water column stratification calculated from temperature profiles) (Idso 1973), lake water temperature (WT), total phosphorus (TP), total nitrogen (TN), chlorophyll-a (hl-a), suspended solids (SS), Secchi depth (SD), pH and total alkalinity (TA) were measured. Data on regional abiotic variables including daily mean air temperature, wind speed, solar irradiance and precipitation are found in Özkan et al. (2014).

2.2. Spatial heterogeneity of environmental variables and phytoplankton communities

We defined spatial heterogeneity as the spatial variability or dissimilarity, depending on the variable (see below), among lakes at each sampling time (Fu et al., 2020). We calculated the spatial heterogeneity for each regional and local abiotic driver as the coefficient of variation (CV: standard deviation divided by the mean of the data) for all lakes at each sampling time. We measured the spatial heterogeneity of zooplankton and phytoplankton communities as the Sørensen dissimilarity coefficient (i.e., overall total beta diversity at the regional scale) among lakes (Baselga, 2010; Legendre, 2014). Then, we partitioned the Sørensen dissimilarity coefficient into two components: the Simpson dissimilarity coefficient (a measure of turnover without influence of richness differences) and the nestedness dissimilarity coefficient (a measure of nestedness resulting from richness differences) of zooplankton communities (Baselga, 2010; Legendre, 2014). We calculated the CV of the PVI index as the spatial heterogeneity of macrophytes across lakes for each year. As the fish sampling frequency only consist of 65 lake years – less than 20% of total lake years for plankton and water environments data, we firstly partitioned 20 years into four periods (i.e., 1: 1989–1993, 2: 1994–1998, 3: 1999–2003, 4: 2004–2008) and then calculated the CV of biomass (kg net-1) and number (no net-1) of piscivores and planktivores as the spatial heterogeneity of fish across lakes for each period. Therefore, we only have spatial heterogeneity of fish for the 1st to 3rd period, because a shift in sampling method in 2004 made it impossible to include fish data after 2003 (Table S1). We computed spatial heterogeneity indices for all variables separately for shallow ($N = 12$, mean depth < 3 m) and deep lakes ($N = 8$, mean depth > 3 m) for each sampling campaign.

2.3. Statistical analysis

We applied generalized additive models (GAM) to extract the seasonal and long-term trends in the time series of the spatial heterogeneity of all abiotic and biotic variables using the “*gam*” function and cubic regression spline from the R-package “*mgcv*” (Wood, 2018). The significance ($P < 0.05$) in the seasonal trends from the GAM results was assessed for each variable, a significant trend indicating occurrence of seasonality. To detect the significance of long-term trends for the spatial heterogeneity of each tested variable, we used GAM to extract the seasonal trends for all variables and then regressed the remaining residuals (hereafter called de-seasonalised residuals) versus year using generalized linear models.

We aimed to assess whether the beta diversity of zooplankton communities is controlled by the combined effects of multiple factors (i.e., phytoplankton beta diversity, regional abiotic variables including mean air temperature, wind speed, solar irradiance and precipitation, and local abiotic variables including water temperature, Schmidt stability, total phosphorus, total nitrogen, Chl-a, suspended solids, Secchi depth, pH and total alkalinity). First, the ordinary least squares regressions were used to model the beta diversity metrics of zooplankton (total beta diversity, spatial turnover, spatial nestedness) as a function of the spatial heterogeneity of climatic and local abiotic variables as well as phytoplankton beta diversity metrics. The de-seasonalised residuals for each variable were used in the models. We also included temporal structure in the models using the *corArma* function (Zuur et al., 2009). Second, the model selection approaches using the second-order Akaike's information criterion (AIC) were applied to select the best models with the most important explanatory variables for the beta diversity metrics. Only models with delta AIC < 2 relative to the best model were selected, as proposed by Burnham and Anderson (2002). We determined pseudo R^2 values (between 0 and 1) as the squared correlation of the linear predictors for each component model (Ferrari and Cribari-Neto, 2004). The sum of Akaike weights including all models was calculated to estimate the relative importance of explanatory variables. The model selection and model averaging were conducted using functions of the “*MuMIn*” package (Barton, 2014).

To assess the relationships between the spatial heterogeneity of zooplankton communities, macrophytes and fish, we firstly calculated the annual mean of zooplankton beta diversity (i.e., de-seasonalised residuals) and then modelled the bivariate relations with general linear regression. As the dataset on macrophyte sand fish (Table S1) had a much lower frequency than those on phytoplankton and zooplankton ($n = 360$), the relationships between zooplankton and macrophytes and fish might be underestimated and should therefore be interpreted with caution.

All statistical tests were conducted separately for shallow and deep lakes using R version 3.51 software (Core, 2013).

3. Results

3.1. Seasonal trends in spatial abiotic and biotic heterogeneity

In the time series (1989–2008), total beta diversity of zooplankton (the Sørensen coefficient) was typically higher in shallow than in deep lakes, which was mainly attributed to higher spatial turnover (i.e., Simpson coefficient) rather than to changes in spatial nestedness (Table 1).

The total beta diversity as well as its two components (i.e., spatial turnover and spatial nestedness) of the zooplankton community exhibited significant seasonal trends (Table 1, Fig. 1) in both shallow and deep lakes. Seasonality explained between 19.2% (spatial nestedness) and 37.3% (spatial turnover) of the variability in the data on shallow lakes and 8.3% (spatial nestedness) and 17.7% (spatial turnover) of the variability in the data on deep lakes (Table 1). For the shallow lakes, the total beta diversity and spatial turnover showed consistent seasonal trends, with more dissimilar zooplankton communities in lakes during summer than in the other seasons. For the deep lakes, the seasonal trends in total beta diversity and the spatial turnover of zooplankton exhibited similar patterns as that of shallow lakes despite of the considerable fluctuations (Fig. 1). However, the seasonal trends were less pronounced for the spatial nestedness of zooplankton in the deep than in the shallow lakes (Fig. 1).

3.2. Long-term trends in spatial abiotic and biotic heterogeneity

For shallow lakes, we found significant temporal decreases in total beta diversity and spatial nestedness and increases in spatial turnover

Table 1
Sørensen coefficient (i.e. total beta diversity), Simpson coefficient (beta diversity ascribed to spatial turnover) and nestedness coefficient (beta diversity ascribed to spatial nestedness-resultant richness differences) during two decades of monitoring. Explained variance (*Var*.exp.) and significance (*P*-value) of seasonal trends (1989–2008) are shown with significant values in bold. All values are reported separately for shallow and deep lakes.

Variables	Shallow lakes				Deep lakes			
	Mean	Range	Var.exp	P.value	Mean	Range	Var.exp	P.value
Total beta diversity	0.76	0.45–0.86	0.317	0.000	0.62	0.23–0.78	0.089	0.000
Spatial turnover	0.65	0.25–0.79	0.373	0.000	0.47	0.08–0.66	0.177	0.000
Spatial nestedness	0.11	0.03–0.5	0.192	0.000	0.14	0–0.56	0.083	0.000

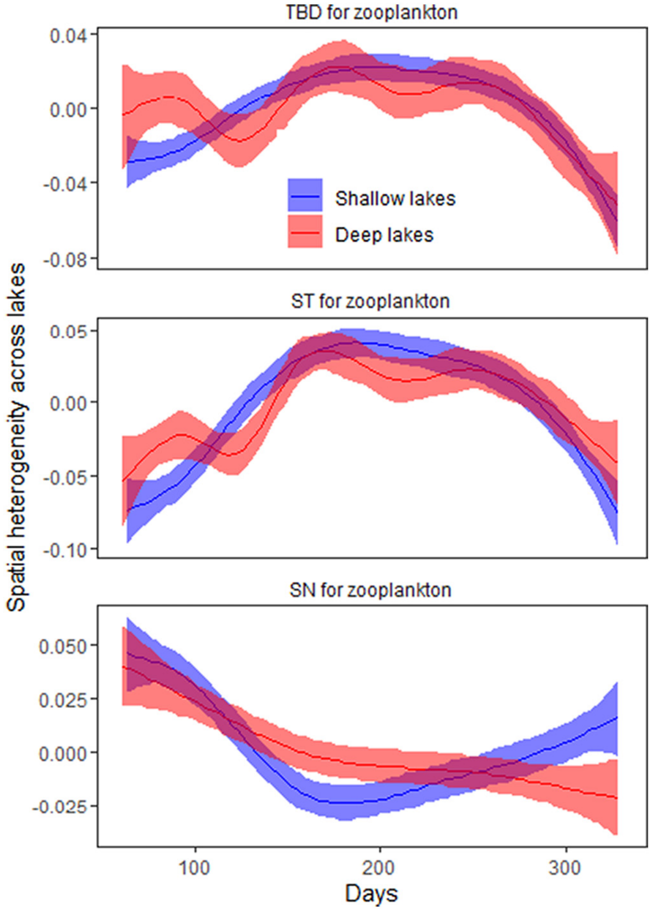

Fig. 1. Seasonal trends (1989–2008) in the three multiple-site beta diversity measures of zooplankton communities: Sørensen dissimilarity (i.e. total beta diversity, TBD), Simpson dissimilarity (beta diversity ascribed to spatial turnover, ST) and nestedness dissimilarity (beta diversity ascribed to spatial nestedness-resultant richness differences, SN) between shallow (blue) and deep (red) lakes. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(Table 2, Fig. 2). For deep lakes, we found significant temporal decreases in total beta diversity and spatial turnover (Table 2, Fig. 2).

By modelling each beta diversity metric of zooplankton, we found that most of the best models retained the beta diversity of phytoplankton as well as both climatic and local abiotic variables (Tables S2 & S3). The best models accounted for 36–37% (shallow lakes) and 28–29% (deep lakes) of the variation in the total beta diversity of zooplankton, for 34–35% (shallow lakes) and 24–25% (deep lakes) in the spatial turnover of zooplankton and 13–14% (shallow lakes) and 8–9% (deep lakes) in the spatial nestedness of zooplankton (Tables S2 & S3). The relative importance and order of explanatory variables retained in the best models of beta diversity metrics differed between shallow and deep lakes (Table 3). A comparison across all possible models showed that the beta diversity of phytoplankton and the CV of pH typically were the most important variables influencing the beta diversity of zooplankton communities in both shallow and deep lakes (Table 3).

Table 2
Linear fit slopes of the linear models for the relationship between the investigated variables and time. Significant slopes are highlighted in bold. Variables are de-seasonalised residuals of the three multiple-site beta diversity measures of zooplankton: Sørensen coefficient (i.e. total beta diversity), Simpson coefficient (beta diversity ascribed to spatial turnover) and nestedness coefficient (beta diversity ascribed to spatial nestedness-resultant richness differences) between shallow and deep lakes.

Variables	Shallow lakes			Deep lakes		
	Slope	P-value	R^2	Slope	P-value	R^2
Total beta diversity	−0.001	0.035	0.010	−0.005	0.000	0.095
Spatial turnover	0.002	0.044	0.009	−0.005	0.000	0.132
Spatial nestedness	−0.003	0.000	0.082	0.000	0.528	−0.002

The total beta diversity of zooplankton was mainly determined by the total beta diversity of phytoplankton, followed by the CV of pH, total alkalinity and total nitrogen across shallow lakes and by the total beta diversity of phytoplankton and the CV of pH, total nitrogen, Schmidt stability across deep lakes (Table 3). The spatial turnover of zooplankton was mostly determined by the spatial turnover of phytoplankton and the CV of pH, total phosphorus and Secchi depth across shallow lakes and by the spatial turnover of phytoplankton and the CV of air temperature, solar irradiance and water temperature across deep lakes (Table 3). The spatial nestedness of zooplankton was mainly determined by the CV of total phosphorus, pH and water temperature across shallow lakes and by the spatial turnover of phytoplankton and the CV of pH, total nitrogen and solar irradiance across deep lakes (Table 3).

The magnitude and directions of each variable in determining the spatial patterns of the zooplankton community differed between shallow and deep lakes. Except for spatial nestedness in shallow lakes, all the three beta diversity measures (i.e., total beta diversity, spatial turnover and spatial nestedness) of zooplankton were strongly positively associated with those of phytoplankton in both shallow and deep lakes (Table 3, Fig. 3). The increases in the CV of pH led to increases in total beta diversity and the spatial turnover of zooplankton in shallow lakes and in the total beta diversity and spatial nestedness of zooplankton in deep lakes, while decreases in the spatial nestedness of zooplankton occurred in shallow lakes (Table 3, Fig. S2). The decreases in the CV of total phosphorus resulted in increases in the spatial turnover and decreases in the spatial nestedness of zooplankton in shallow lakes (Table 3). The decreases in the CV of total nitrogen caused decreases in the total beta diversity of zooplankton in shallow lakes and increases in the total beta diversity as well as the spatial nestedness of zooplankton in deep lakes (Table 3).

3.3. Effects of macrophyte and fish on spatial heterogeneity of zooplankton

We found significant annual decreases in the spatial heterogeneity of macrophytes in shallow lakes but not in deep lakes (Table 4, Fig. S3). A significant temporal decrease in the spatial heterogeneity of fish (i.e., piscivores and planktivores) biomass and number were found in both shallow and deep lakes (Table 4), with exception of planktivores biomass and number as well as total fish number in shallow lakes. Except for spatial nestedness in deep lakes, the three beta diversity measures of zooplankton were strongly and positively correlated with the spatial heterogeneity of PVI in both shallow and deep lakes, explaining 41–78% of the variation of the annual trends in spatial zooplankton heterogeneity (Table 5). In shallow lake, the spatial heterogeneity of piscivores by biomass and number was negatively associated with the spatial turnover of zooplankton (26–27%) and positively with the spatial nestedness of zooplankton (51–53%) (Table 5). In deep lakes, the spatial heterogeneity of fish (i.e., piscivores and planktivores) biomass and number had a strongly positive association with the spatial turnover (57–65%) and total beta diversity (26–37%) of zooplankton (Table 5).

4. Discussion

Spatial turnover (i.e., Simpson coefficient) rather than spatial nestedness dominated the total beta diversity (i.e., Sørensen coefficient) of zooplankton communities, suggesting that zooplankton community dissimilarities among lakes could mainly be attributed to taxon replacement. This is in accordance with previous findings on other aquatic biota such as macrophytes, fish, macroinvertebrates and phytoplankton (Al-Shami et al., 2013; Alahuhta et al., 2017; Fu et al., 2019; Fu et al., 2020; López-Delgado et al., 2020). In our study, the physio-chemical

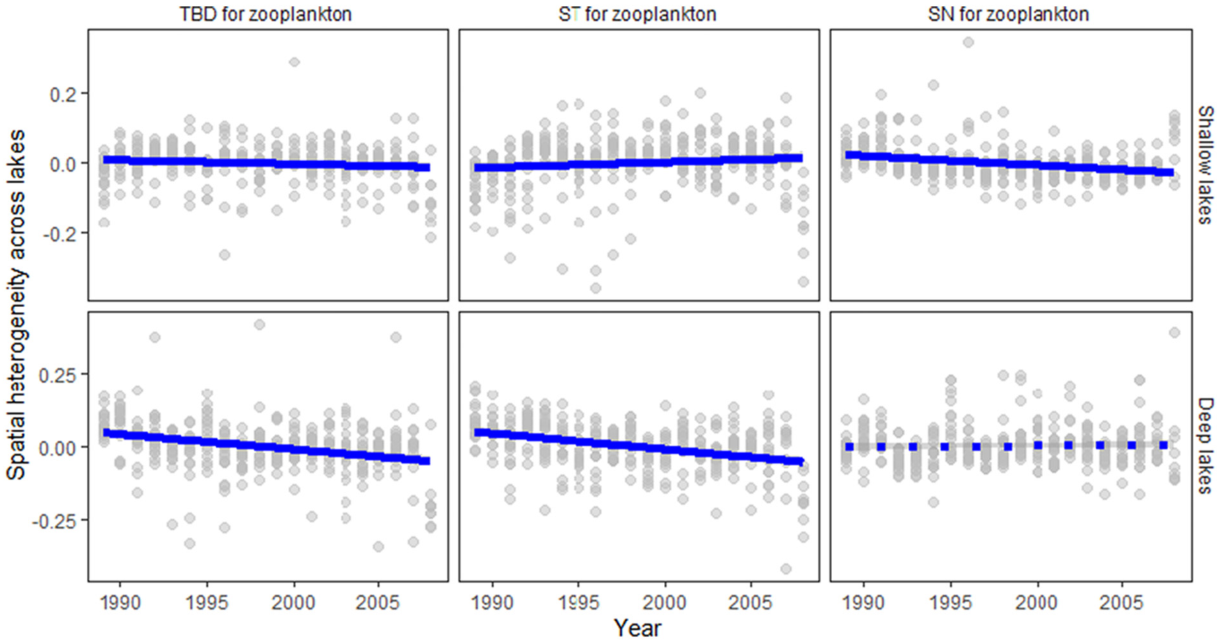

Fig. 2. Long-term trends (1989–2008) in de-seasonalised residuals (residuals from GAM models extracting seasonal trends for each variable) of the three multiple-site beta diversity measures of zooplankton communities: Sørensen coefficient (total beta diversity, TBD), Simpson coefficient (beta diversity ascribed to spatial turnover, ST) and nestedness coefficient (beta diversity ascribed to spatial nestedness-resultant richness differences, SN). Regression lines are drawn in blue. Solid line indicates significant relationships and dashed line non-significant relationships. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

variability, especially for nutrient concentrations (e.g., TP ranged from 0.001 to 2.7 mg L^{-1}, see Table 1 in Özkan et al. (2014)), among the studied lakes may have formed a range of specific habitats with dissimilar ecosystem properties (e.g., productivity, water transparency etc.) and thus different zooplankton communities in the landscape, leading to the observed pronounced importance of spatial turnover.

We found significant seasonality in the spatial heterogeneity of zooplankton communities, with the strongest seasonal trends emerging in the shallow lakes. For both lake types, the total beta diversity and spatial turnover of the zooplankton community exhibited a significant peak in summer, while spatial nestedness showed a reverse pattern, which is consistent with our previous findings on phytoplankton communities and TP using the same dataset (Fu et al., 2020). Large heterogeneity of phytoplankton in summer among the lakes (Fu et al., 2020) also suggests availability of more diverse food resources for the zooplankton, which may have caused the peak in the spatial turnover of zooplankton in summer. Moreover, the differences in the magnitude of macrophyte growth and expansion in summer among the lakes (Table S1) might

Table 3

Relative importance (*RI*) of explanatory variables for all model compilations and standardised coefficients (*beta*) obtained from model averaging over all combinations of model terms. Models were developed for the three multiple-site beta diversity measures: Sørensen coefficient (i.e. total beta diversity), Simpson coefficient (beta diversity ascribed to spatial turnover) and nestedness coefficient (beta diversity ascribed to spatial nestedness-resultant richness differences). The measures of phytoplankton included in each model were accordingly the same as those of zooplankton (e.g., spatial turnover of phytoplankton was included as a predictor modelling the spatial turnover of zooplankton). All variables are de-seasonalised residuals (residuals from GAM models extracting seasonal trends for each variable). For *RI*, 1.00 indicates that this particular variable is selected in all models, whereas 0 means that the variable is not selected in any of the models. *Beta* indicates the directions between the beta diversity coefficient and the environmental variable. If a given variable (not shown in the table) was not included in the most important beta diversity models (AICc <2.0), the direction of influence was obtained from a full model including all the variable candidates. The most important predictors of each metric are given in bold, and the marginally important predictors of each metric are shown in italics. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Predictors	Shallow lakes						Deep lakes					
	Total beta diversity		Spatial turnover		Spatial nestedness		Total beta diversity		Spatial turnover		Spatial nestedness	
	RI	Slope	RI	Slope	RI	Slope	RI	Slope	RI	Slope	RI	Slope
Phytoplankton beta diversity	**1.00**	**0.619**	**1.00**	**0.742**	0.22	0.028	**1.00**	**0.801**	**1.00**	**0.494**	**1.00**	**0.523**
Regional variables												
Air temperature	0.86	0.013	0.83	0.018	0.03	0.000	0.10	−0.001	**1.00**	**−0.031**	0.78	0.016
Solar irradiance	0.12	0.003							**1.00**	**−0.126**	**1.00**	**0.128**
Precipitation	0.05	0.000							0.05	0.000		
Wind speed	0.06	0.002	0.07	0.003	0.72	−0.063	0.07	0.002	0.05	0.001		
Local variables												
Water temperature			0.67	−0.035	**1.00**	**0.068**	0.92	0.067	**1.00**	**0.082**		
Schmidt stability	0.13	0.000	0.74	0.007	0.78	−0.005	**1.00**	**0.028**	0.84	0.018	0.44	0.006
Total phosphorus			**1.00**	**−0.059**	**1.00**	**0.057**	0.11	−0.002	0.05	−0.001	0.27	0.005
Total nitrogen	**0.85**	**0.023**	0.18	0.003	0.03	0.000	**1.00**	**−0.127**	0.02	0.000	**1.00**	**−0.074**
Chlorophyll-a			0.12	0.001	0.03	0.000	0.91	−0.031	0.26	0.004	0.59	−0.009
pH	**1.00**	**0.191**	**1.00**	**0.280**	**1.00**	**−0.192**	**1.00**	**0.704**	0.56	0.199	**1.00**	**0.459**
Secchi depth	0.06	0.000	**1.00**	**−0.044**	0.74	0.017	0.11	−0.004	0.13	0.003	0.34	−0.013
Suspended solids			0.06	0.001	0.03	0.000	0.81	0.023	0.73	0.014	0.08	0.001
Alkalinity	**1.00**	**0.058**			0.09	0.002	0.92	0.097	0.08	0.003	0.61	0.048

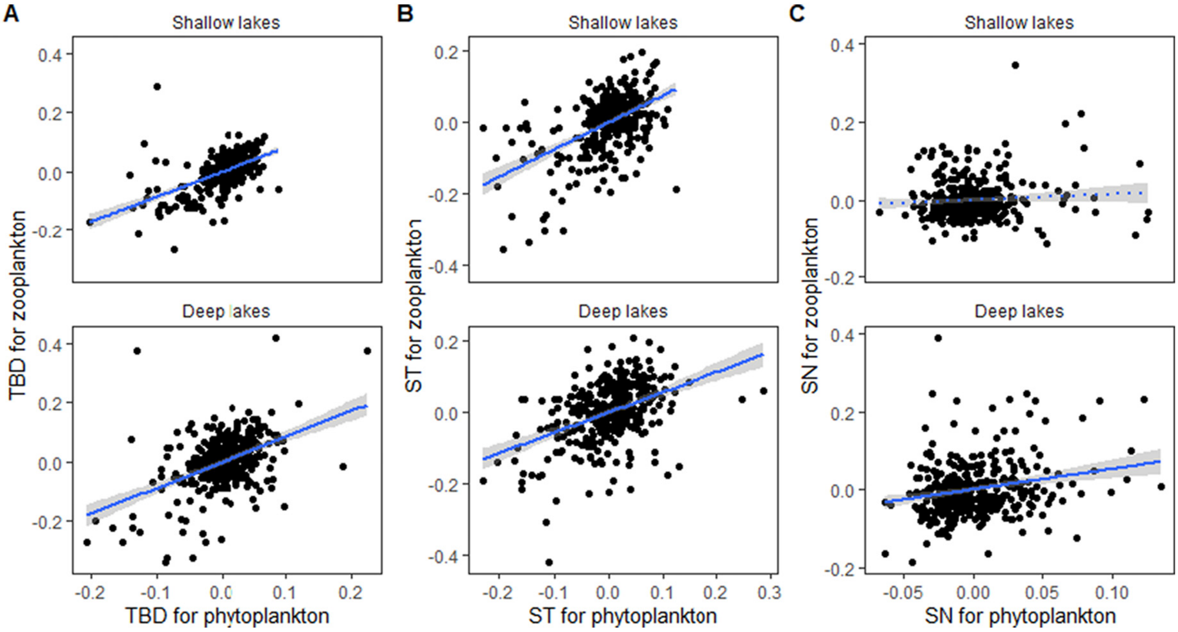

Fig. 3. Relationships between the three multiple-site beta diversity measures of zooplankton communities: Sørensen coefficient (total beta diversity, TBD), Simpson coefficient (beta diversity ascribed to spatial turnover, ST) and nestedness coefficient (beta diversity ascribed to spatial nestedness-resultant richness differences, SN) of phytoplankton and zooplankton in shallow and deep lakes, respectively. Regression lines are drawn in blue. Solid line indicates significant relationships and dashed line non-significant relationships. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

have created the high habitat heterogeneity observed in summer in some of the lakes, heterogeneity remaining low for others. In addition, the differences in fish community composition among the lakes (Jeppesen et al., 2000) might cause variation in the predation pressures on zooplankton. Therefore, both macrophytes and fish might have contributed to the high turnover of the zooplankton community in summer. The less pronounced seasonality of spatial zooplankton heterogeneity in the deep lakes likely reflects the limited effects of macrophytes on zooplankton collected in the open water and the typically lower predation pressure from planktivorous fish (Jeppesen et al., 1997).

We found significant temporal decreases in the total beta diversity of zooplankton in both the shallow and the deep study lakes, indicating that more homogenous zooplankton communities may have developed after two decades of restoration (e.g., external nutrient loading reduction, occasionally supplemented with biomanipulation) at regional scale. Previous findings have reported that zooplankton communities in hypereutrophic lakes become more heterogeneous after a strong decrease in nutrient loading (Özkan et al., 2016), as is also the case in meso-oligotrophic lakes, increasing the similarity of zooplankton communities among lakes. This is supported by the results from local-scale studies revealing that an increase in zooplankton functional diversity with declining TP could be attributed to high spatial heterogeneity (vertical) of phytoplankton resources (especially of cyanobacteria) as well as dominance by diatoms/chrysophytes at low TP (Barnett and Beisner, 2007). According to the model selection results, the spatial heterogeneity of phytoplankton was the most important variable determining the long-term changes in the spatial heterogeneity of zooplankton. As the nutrient loadings were proportionally lower during the study period in the most hypertrophic lakes than in the less eutrophic lakes (Özkan et al., 2016), the phytoplankton communities became more similar among the lakes (Fu et al., 2020), with implications also for the zooplankton community similarity. In addition, our previous studies showed that reduced water TP and TN concentrations are the dominant reasons for the diminished spatial heterogeneity of phytoplankton across lakes (Fu et al., 2020). Moreover, Özkan et al. (2014) found that the congruence between phytoplankton and zooplankton community increases greatly with decreasing nutrient levels at the local scale, suggesting increasing correlation across trophic levels during lake recovery from eutrophication. Therefore, the strongly positive association between the spatial heterogeneity of phytoplankton and zooplankton provides further evidence of the assumption that bottom-up forces (i.e., nutrients → phytoplankton → zooplankton) drive zooplankton community compositional changes at regional scale.

The temporal decreases in the spatial heterogeneity of macrophytes explained a significant part of the variation in the spatial heterogeneity of zooplankton in the shallow lakes. In the beginning of the study period, the distribution of macrophytes differed more pronouncedly among the lakes, ranging from limited coverage or plant absence in the most eutrophic lakes to large coverage of plants in some meso-oligotrophic lakes (Lauridsen et al., 2003; Søndergaard et al., 2010). After two decades of restoration, macrophytes have colonised some of the eutrophic shallow lakes (Jeppesen et al., 2005b; Søndergaard et al., 2010), leading to lower dissimilarity of macrophyte distribution among the lakes. Macrophytes provide refuges for zooplankton against fish predation, thereby increasing the survival of some sensitive pelagic zooplankton taxa (e.g. *Daphnia* spp.), especially large-bodied crustaceans (Jeppesen et al., 1998b). In addition, macrophyte beds constitute heterogeneous habitats due to their highly complex spatial architecture in the water column, and they thus provide various niches for the growth and reproduction of zooplankton, especially for benthic and plant-associated taxa (Burks et al., 2006; Lauridsen et al., 1996). Therefore,

Table 4

Results of the linear models on the relationship between the coefficient variations of the investigated variables and time. PVI indicates plant volume infested. Statistically significant relationships were in bold.

Variables	Shallow lakes			Deep lakes		
	Slope	P-value	R^2	Slope	P-value	R^2
PVI	**−0.053**	**0.026**	**0.26**	−0.027	0.303	0.01
Piscivores biomass (kg net^{-1})	−1.265	<0.001	0.74	−0.597	<0.001	0.64
Piscivores number (no. net^{-1})	−0.909	<0.001	0.78	−0.686	<0.001	0.99
Piscivores proportion (%)	−0.401	<0.001	0.72	−0.202	<0.001	0.94
Planktivores biomass (kg net^{-1})	0.052	0.212	0.05	−0.623	<0.001	0.67
Planktivores number (no. net^{-1})	0.068	0.094	0.14	−0.709	<0.001	0.78
Total fish biomass (kg net^{-1})	−0.066	<0.05	0.33	−0.609	<0.001	0.62
Total fish number (no. net^{-1})	−0.004	0.823	<0.01	−0.698	<0.001	0.71

Table 5

Results of the linear models for the relationship between the coefficient variation of PVI (plant volume infested), piscivores biomass, number and proportion, planktivores biomass and number, and the three multiple-site beta diversity measures: Sørensen coefficient (i.e. total beta diversity), Simpson coefficient (beta diversity ascribed to spatial turnover) and nestedness coefficient (beta diversity ascribed to spatial nestedness-resultant richness differences), respectively.

Predictors	Shallow lakes						Deep lakes					
	Total beta diversity		Spatial turnover		Spatial nestedness		Total beta diversity		Spatial turnover		Spatial nestedness	
	Slope	R^2	Slope	R^2	Slope	R^2	Slope	R^2	Slope	R^2	Slope	R^2
PVI	0.057***	0.73	0.089***	0.73	−0.032**	0.41	0.081***	0.57	0.078***	0.6	0.002	<0.01
Piscivores biomass	0.001	<0.01	−0.014*	0.26	0.015**	0.51	0.037*	0.36	0.046***	0.60	−0.011	<0.01
Piscivores number	0.001	<0.01	−0.020*	0.27	0.022**	0.53	0.035*	0.26	0.049***	0.58	−0.016	0.02
Piscivores proportion	0.003	<0.01	−0.042	0.25	0.046**	0.50	0.131*	0.34	0.171***	0.65	−0.051	0.01
Planktivores biomass	−0.022	<0.01	0.054	<0.01	−0.073	0.08	0.042*	0.36	0.046***	0.60	−0.011	<0.01
Planktivores number	−0.020	<0.01	0.069	0.02	−0.089$^{\phi}$	0.15	0.035**	0.37	0.044***	0.63	−0.012	<0.01
Total fish biomass	−0.031	<0.01	−0.124	0.08	0.108	0.09	0.036*	0.36	0.044***	0.57	−0.011	<0.01
Total fish number	−0.057	<0.01	−0.012	<0.01	−0.029	<0.01	0.033*	0.37	0.043***	0.61	−0.011	<0.01

$^{\phi}$ $P < 0.1$.
* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

the effects of the increased number of refuges and niches may have enhanced the zooplankton diversity in the most eutrophic lakes experiencing macrophytes recovery at local scale, leading to increased similarity of the zooplankton communities among shallow lakes at the regional scale. Remarkably, a positive correlation between the spatial heterogeneity of macrophytes and zooplankton was also observed in deep lakes (Fig. 4) despite that no clear temporal decreases occurred in the spatial heterogeneity of macrophytes (Table 4, Fig. S3). This might be attributed to the fact that the increase in macrophyte PVI was relatively small in some of the hypertrophic deep lakes, preventing observation of temporal changes in spatial heterogeneity of macrophytes (Fig. S4). However, the abundance of zooplankton could also be greatly promoted by minor increases in macrophytes at local scale, especially in lakes shifting between presence and absence macrophytes (Jeppesen et al., 1998b; Kuczyńska-Kippen and Joniak, 2016; Onsem et al., 2010), which reduces the spatial heterogeneity of zooplankton at the regional scale.

Surprisingly, the long-term trends in the spatial zooplankton heterogeneity in the shallow lakes were independent of the spatial heterogeneity of planktivores, even though planktivorous fish as well as macrophytes often exert dual and interacting controls on zooplankton communities (Jeppesen et al., 1997). This could be attributed to that macrophyte has recolonized in most lakes and provide more similar habitats for zooplankton across shallow lakes, which is also evidenced by the reduced top-down control by planktivorous fish in lakes rich in submerged macrophytes (Jeppesen et al., 1997). However, the temporal decreases in the spatial heterogeneity of piscivores caused significant increases in spatial turnover and decreases in spatial nestedness of zooplankton, which may thus entail an invariable response of total beta diversity of zooplankton in the shallow lakes. In the deep lakes, temporal decreases in the spatial heterogeneity of both piscivores and planktivores led to a strong decrease in the total beta diversity as well as the spatial turnover of zooplankton. Notably, previous findings in Danish lakes overall report that temporal changes in fish community composition take place as a response to either reduced external nutrient loading or biomanipulation, in the form of an increase in the proportion of piscivorous fish and a decrease in the share of planktivorous fish (Jeppesen et al., 2005a). In addition, a shift occurred towards dominance by piscivorous fish species characteristic of less eutrophic waters, which thus lead to homogenous

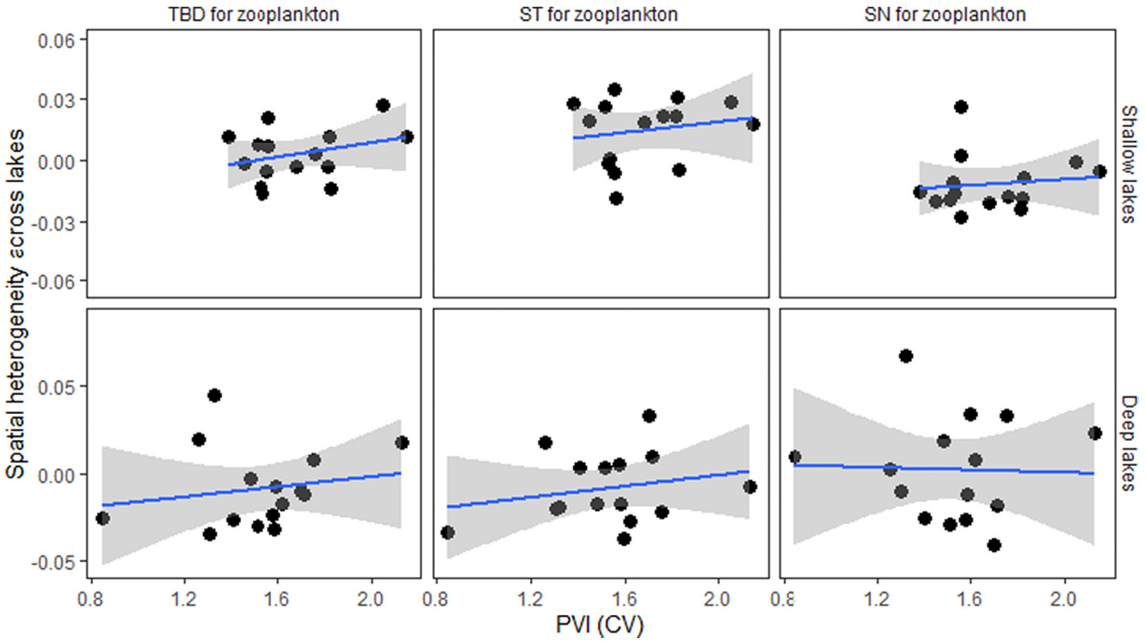

Fig. 4. Relationships between the coefficient variation of PVI (plant volume infested) for macrophytes and the three multiple-site beta diversity measures of zooplankton communities: Sørensen coefficient (total beta diversity, TBD), Simpson coefficient (beta diversity ascribed to spatial turnover, ST) and nestedness coefficient (beta diversity ascribed to spatial nestedness-resultant richness differences, SN) of zooplankton in shallow and deep lakes, respectively. Regression lines are drawn in blue. Solid line indicates significant relationships and dashed line non-significant relationships. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

fish community among lakes (Jeppesen et al., 2005a). Furthermore, the observed increases in the body weight of cladocerans and the zooplankton to phytoplankton biomass ratio during summer in eutrophic lakes are indicative of reduced top-down control on zooplankton during the recovery from eutrophication (Jeppesen et al., 2005a; Jeppesen et al., 2005b). Therefore, our results suggest that the temporal changes in top-down forces from the changes of fish community could have important controls on the spatial heterogeneity of zooplankton across a landscape.

Besides biotic drivers, we also found that abiotic variables contributed significantly to the variations of temporal changes in the spatial heterogeneity of zooplankton at regional scale. This is consistent with previous results revealing environmental heterogeneity to be a major controller of biotic heterogeneity. However, the magnitude and direction of abiotic variables in determining the spatial heterogeneity of zooplankton a regional scale were largely dependent on abiotic variables, beta diversity measures and water depth. For example, the total beta diversity of zooplankton was strongly positively associated with spatial TN heterogeneity in the shallow lakes but negatively so in the deep lakes (Table 3), although temporal decreases in spatial TN heterogeneity occurred in both the shallow and the deep lakes. In addition, the spatial turnover of zooplankton was positively influenced by pH and negatively by TP and Secchi depth in the shallow lakes positively influenced by water temperature and negatively by air temperature and solar irradiance in the deep lakes (Table 3). In both the shallow and deep lakes, however, all of these abiotic variables showed significant temporal decreases in spatial heterogeneity at regional scale, which is consistent with the temporal trends in the spatial heterogeneity of zooplankton. The observed results (opposite directions) between shallow and deep lakes may reflect that abiotic variables exert control on zooplankton through multiple pathways that involve both direct and indirect effects (e.g., phytoplankton, macrophytes and fish). In our previous study, both the regional and local variables had direct and indirect effects on the spatial heterogeneity of phytoplankton (Fu et al., 2020), forming a bottom-up force that affected the zooplankton community. Furthermore, the abundance and fish communities and their composition varied greatly along the gradients of trophic state, water depth and climate (Beisner et al., 2006; Jeppesen et al., 2005a; Liu et al., 2014; López-Delgado et al., 2020), which help to explain the changes among lakes in the spatial heterogeneity of zooplankton caused by a distinct predation pressure (i.e., top-down force).

5. Conclusion

Our study indicates that the temporal decreases in spatial the heterogeneity of zooplankton communities in lakes recovering from eutrophication were mostly determined by reduced spatial heterogeneity of phytoplankton and macrophytes at regional scale, reflecting largely the reduced external nutrient loading to the most hypertrophic lakes. As the spatial heterogeneity of phytoplankton is greatly affected directly or indirectly by the spatial heterogeneity of TP and TN (Fu et al., 2020), our results further highlight the role of bottom-up forces in regional zooplankton community patterns. The significant decrease in external nutrient loading to the hypertrophic lakes largely increased water transparency and thus promoted macrophyte restoration at local scale (Lauridsen et al., 2003), enhancing the similarity of zooplankton habitats between lakes (Burks et al., 2006; Lauridsen et al., 1996). In addition, also abiotic variables were important for determining the spatial heterogeneity of zooplankton. The consistent decreases in the spatial heterogeneity of macrophytes as well as abiotic variables exert a combined effect of environmental (i.e., abiotic and biotic) heterogeneity on zooplankton community patterns at regional scale. Furthermore, we detected significant top-down effects of changes in fish community structure on spatial patterns of zooplankton as expected. Overall, the restoration measures implemented to reduce the external nutrient loading to Danish lakes have decreased the abiotic and biotic heterogeneity (i.e., phytoplankton, zooplankton, macrophytes, and fish) across lakes at regional scale; this despite the increased heterogeneity at local scale between some hypereutrophic lakes subjected to major loading reductions (Özkan et al., 2016). Too few data from fish and less frequent macrophytes sampling were available for assessing the relative role of bottom-up and top-down forces on temporal dynamics of zooplankton heterogeneity. Therefore, different patterns may emerge when involving isochronous dataset from plankton, fish, macrophytes as well as environments and much more lakes across a regional or global scale.

Data availability

Data are from the national survey program and can be obtained from https://danmarksmiljoeportal.ze 861ndesk.com/hc/da

CRediT authorship contribution statement

Hui Fu: Conceptualization, Methodology, Formal analysis, Data curation, Writing – original draft, Funding acquisition. **Korhan Özkan:** Data curation, Writing – review & editing. **Guixiang Yuan:** Funding acquisition, Writing – review & editing. **Liselotte Sander Johansson:** Methodology, Investigation, Writing – review & editing. **Martin Søndergaard:** Conceptualization, Investigation, Methodology, Writing – review & editing. **Torben L. Lauridsen:** Conceptualization, Investigation, Methodology, Writing – review & editing. **Erik Jeppesen:** Conceptualization, Investigation, Methodology, Writing – review & editing, Supervision, Funding acquisition, Project administration.

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.

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