

Patterns of Seasonal Stability of Lake Phytoplankton Mediated by Resource and Grazer Control During Two Decades of Re-oligotrophication

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ABSTRACT

Human-induced changes in external nutrient loading affect the phytoplankton community and abundance directly by changing the amount of nutrients available, but also indirectly through changes in the zooplankton (that is, grazer) community structure, mediated in part by changes in the fish community structure and biomass. Such shifts affect the species dynamics and community succession of lake phytoplankton communities, and they may ultimately influence community stability. However, the relative importance of different biotic mechanisms influencing the community stability of phytoplankton along nutrient and associated zooplankton grazing pressure gradients

remains unclear. Here, we evaluated the importance of four potential stabilizing biotic metrics—taxon richness, synchrony, community dominance and biomass of phytoplankton to the seasonal stability over two decades of re-oligotrophication in 20 Danish lakes. We found no clear temporal patterns in seasonal stability across lakes but considerable variations in the individual lakes. Total phosphorus (TP) affected the seasonal stability of the phytoplankton communities either directly or indirectly through changes in community dominance. Total nitrogen (TN) influenced the seasonal stability indirectly via changes in phytoplankton taxon richness, synchrony, and community dominance. Grazer richness (that is, zooplankton taxa richness) impacted the seasonal stability indirectly through changes in phytoplankton taxon richness and synchrony. Grazing pressure, using the biomass ratio of zooplankton:phytoplankton as a proxy, had an indirect effect on seasonal stability via changes in synchrony and community dominance. Compensatory dynamics (as indicated by the synchrony of phytoplankton) exerted dominant control of phytoplankton sea-

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sonal stability at high TN and high grazer richness and pressure, while the portfolio effect (as indicated by taxon richness) contributed to phytoplankton seasonal stability at low TN and high grazer richness. However, a strongly negative selection effect (as indicated by community dominance of phytoplankton) was observed at high nutrient levels and low grazer richness. Grazer richness and grazing pressure had stronger stabilizing effects on the seasonal succession of the phytoplankton communities than did TP and TN. Our results highlight how various biotic mechanisms (for example, compensatory dynamics and portfolio effect) can change in their importance in maintaining the seasonal stability of phytoplankton communities subjected to nutrient and grazer control.

Key words: Danish lakes; Nutrients; Compensatory dynamics; Portfolio effect; Selection effect; Top-down control.

INTRODUCTION

What underpins the temporal stability of natural communities in the face of human-induced environmental changes has received much attention (Tilman and others 2005; Hautier and others 2015). Several mechanisms have been suggested to stabilize species or community dynamics through time in response to environmental variations (Lehman and Tilman 2000; Hooper and others 2005; Tilman and others 2006; Donohue and others 2016). Most previous studies have strongly focused on the stabilizing effects of diversity [for example, portfolio effects suggesting that diversity promotes stability (Doak and others 1998)] as well as community dominance [for example, selection effects that are suggested to strengthen the impacts of dominant species on stability (Loreau and others 2001; Hillebrand and others 2008)] and abundance [for example, over-yielding effects predicting that a greater temporal mean relative to variation of community abundance improves stability (Hector and others 2010)]. Importantly, all of these hypothesized community stabilizing mechanisms require high diversity to function (Hooper and others 2005). Nevertheless, recent studies have shown that community stability largely depends on the compensatory dynamics between different individual populations (Loreau and de Mazancourt 2013) where the asynchronous responses of species to fluctuating environments lead to negative

covariance within communities, producing high community stability over time (Hector and others 2010). As the species and community dynamics not only track the changes in environmental conditions but also have important consequences for stability (Tilman 1999; Roscher and others 2011), there is a growing awareness of how changes in management (for example, re-oligotrophication) of ecosystems can stabilize biotic communities (Emily and others 2010; Hallett and others 2014).

Lake biotic communities have been widely reported to vary markedly with changes in external nutrient loading (for example, Jeppesen and others 2005). Phytoplankton communities not only closely reflect the nutrient level at either an annual or a seasonal scale (Anneville and others 2005; Soendergaard and others 2005; Salmaso 2010; Winder and Cloern 2010), they also show a congruent response with zooplankton communities (Özkan and others 2014). From oligotrophic to hypereutrophic conditions, lake phytoplankton communities show marked changes in diversity and abundance due to distinct responses of phytoplankton taxa with increased nutrient concentrations in the water, ultimately leading to dominance of a few species (for example, cyanobacteria or green algae) (Feuchtmayr and others 2009; Xu and others 2010; Harper 2012). In the reverse process of re-oligotrophication, however, phytoplankton often exhibit a time-lagged response to management efforts introduced to reduce the nutrient inflow into lakes, partly reflecting continued release of phosphorus from the sediments (Jeppesen and others 2002; Søndergaard and others 2003; Anneville and others 2004; Köhler and others 2005; Özkan and others 2016). In addition, internal loading has been suggested to greatly delay the recovery, as a new equilibrium for TP is not reached until after 10–15 years for most lakes (Jeppesen and others 2005). This, in turn, might lead to changes in phytoplankton community composition but not necessarily in phytoplankton biomass. The resilience of phytoplankton biomass to re-oligotrophication might reflect a stabilizing effect of diversity and compensatory dynamics (Anneville and others 2005; Jochimsen and others 2013; Baert and others 2016). Phytoplankton communities are characterized by being highly diverse in terms of species and function, and the communities may therefore show diversified responses to environmental fluctuations and changes in grazer community dynamics (Reynolds 1984; Litchman and Klausmeier 2008). Previous studies have indicated that phytoplankton species differ in their responses to changing nutrient con-

ditions and grazer community structure (that is, size, abundance), displaying compensatory dynamics within the communities (Vasseur and Gaedke 2007; Jochimsen and others 2013). For instance, a red-colored filamentous and toxic cyanobacterium, *Planktothrix rubescens*, declined sharply whereas *Dinobryon* spp., *Rhodomonas*, *Cryptomonas* and a variety of different diatoms tended to increase with decreasing phosphorus concentrations (due to restoration measures) in Lake Bourget (France), with zooplankton grazing also being considered as an important driver (Jacquet and others 2014). In Lake Constance (Bodensee), edible and less edible phytoplankton exhibited compensatory dynamics at high grazing pressure and low nutrient concentrations during the growth seasons (Vasseur and others 2005). Thus, the temporal variability of phytoplankton is largely determined by the mixed impacts of nutrients and herbivore grazing (Jeppesen and others 1997; Cottingham and others 2004), especially during the growing season.

Likewise, at short time scales, significant seasonality has been reported in both the community biomass and composition of phytoplankton (Jeppesen and others 2002; Anneville and others 2004; Winder and Cloern 2010), usually reflecting strong coherence with environmental changes (for example, nutrients, water temperature, light) and congruence with changes in the zooplankton community (Özkan and others 2016). Long-term lake re-oligotrophication accompanied by climate warming has resulted in plastic changes in the seasonal patterns of phytoplankton community succession and temporal shifts in life history events (for example, phenology) of phytoplankton species (Anneville and others 2005, 2018). Moreover, the congruent development of zooplankton communities might also contribute to variations in the grazing pressure on phytoplankton, leading to shifts in species phenology and in the seasonal succession of phytoplankton communities (Jeppesen and others 2005; Vasseur and others 2005; Huber and Gaedke 2006; Özkan and others 2014). Such modification of species phenology is largely due to the different sensitivity of phytoplankton species to environmental changes and grazer control (Cottingham and Schindler 2000; Vasseur and others 2005; Anneville and others 2019), but major seasonal variation in phytoplankton biomass (that is, annual mean seasonal variability of phytoplankton biomass divided by standard deviation) may not necessarily follow (Anneville and others 2005). Thus, species-level dynamics may not only contribute to plasticity in the seasonal succession of

phytoplankton; it may also have a stabilizing effect at the community level (Walters and others 2013). Although the occurring re-oligotrophication processes have caused marked changes in the in-lake nutrient level as well as in grazer community dynamics at both seasonal and annual scales, the relative importance of different biotic mechanisms in maintaining seasonal stability under ongoing reductions in external nutrient loading has yet to be explored.

The objective of this study was to examine the biotic stabilizing mechanisms that govern the seasonal succession of the phytoplankton community and relate them to nutrients and grazer control. To do this, we used a long-term field monitoring dataset (1989–2008) on 20 Danish lakes that underwent significant reductions in external nutrient loading during this period. Previous studies based on these lakes indicated significant decreases in nutrient concentrations (total phosphorus and nitrogen, TP and TN) and phytoplankton biomass and increases in water transparency, phytoplankton taxon richness, and grazer (that is, zooplankton) richness and pressure (that is, the ratio between zooplankton and phytoplankton biomass) (Soendergaard and others 2005; Jeppesen and others 2005; Özkan and others 2014; Özkan and others 2016). Remarkably, marked changes in the seasonal succession and plasticity in the phenology of phytoplankton community were observed in the investigated lakes during re-oligotrophication (Jeppesen and others 2002). In this study, we focused on how phytoplankton seasonal stability varied with resource gradients (that is, TP and TN) and with grazer richness (that is, richness of zooplankton) and grazing pressure (that is, zooplankton:phytoplankton biomass ratio) and on the relative importance of four biotic stabilizing mechanisms—portfolio, selection, compensation, and over-yielding effect—in determining the seasonal stability. Specifically, we aimed to elucidate how TP and TN as well as grazer richness and pressure influence the seasonal stability of phytoplankton either directly or indirectly through changes in species and community dynamics (for example, species diversity, dominance, synchrony, and community biomass) during re-oligotrophication.

METHODS

Data Collection

Twenty lakes were monitored between 1989 and 2008 as part of the Danish monitoring program on

the aquatic environment (NOVANA). Twelve of the lakes are shallow with a mean depth below 3 m, and eight lakes are deeper (mean depth 3.02 to 15.08 m) (Figure S1). The area and hydraulic retention time of the lakes ranged from 0.11 to 39.54 km² and from 0.01 to 7.5 year, respectively (Table S1). Overall, the most diverse group was chlorophytes for phytoplankton and rotifers for zooplankton (Özkan and others 2014). During the studied period, air temperature increased significantly, especially in summer, whereas no significant long-term trend was observed in water surface temperature and water column stability in the study lakes (Özkan, and others 2016). Phytoplankton community composition shifted dramatically from high dominance by Chlorophyta and Cyanobacteria to high evenness with more diverse genera, especially in the lakes experiencing strong declines in water nutrient concentrations (Özkan and others 2016). Concomitantly, for zooplankton, decreased Rotifera and Copepoda dominance and increased Cladocera proportions were observed (Özkan and others 2016).

Phytoplankton and water were sampled bi-weekly during summer (May–October) and once a month during winter (December–February) at mid-lake depth-integrated sites in the photic zone. Zooplankton densities were determined using depth-integrated water samples taken with a Patalas sampler (from the top to the bottom) from three mid-lakes stations and pooled. Depending on the total phosphorus (TP) level, between 4.5 and 9 L of the pooled sample were filtered through an 80-mm net and fixed in Lugol's iodine. For some lakes, winter data are missing because the lakes were frozen. The phytoplankton were counted and their biomass estimated based on size and shape. Details on sampling, identification, and counting of plankton and on the sampling and measurements of lake environmental variables and climate variables can be found in Özkan and others (2014) for 17 of the 20 lakes, whereas the sampling methods and frequency for the remaining three lakes (Furesø Storesø, Engelsholm Sø, Kvie Sø) followed the same protocol. We screened the plankton data for potential inconsistencies and made corrections using an inclusive approach (Özkan and others 2014). All taxa were aggregated to genus level due to varying levels of species identification between the different plankton groups and potential differences in the identification skills of the taxonomists. The alternative genus level classification of plankton has been suggested as reliable predictors of species level richness, and perform well in the richness-environment and assemblage-environment

relationships in freshwater ecosystems (Gallego and others 2012; Sodr e and others 2020), and the congruence between taxon and species would increase with increased species:genus and species:family ratios (Gallego and others 2012).

Statistical Analyses

We calculated annual mean values of total phosphorus (TP) and total nitrogen (TN) for each lake. In addition, we measured grazer richness and grazing pressure as the annual mean values of the taxon number of zooplankton and the biomass ratio between zooplankton and phytoplankton.

We measured the seasonal stability (μ/σ) of the phytoplankton community as the ratio of annual mean biovolume (μ) relative to annual standard deviation (σ) for each year during the study period (1989–2008). We calculated four metrics—taxon richness (portfolio effect), dominance (selection effect), synchrony, and community biomass (overyielding effect)—to characterize the four biotic mechanisms driving community stability. We calculated taxon richness and community biomass as the annual mean values of the taxon number and the biovolume of the phytoplankton community present in each lake. We calculated the annual mean of Simpson's dominance index ($D = 1 - \sum_{i=1}^S p_i^2$), where p_i is the proportion of species i , and S is the number of species, to quantify the community dominance for each lake. Species synchrony was used as an index of compensatory dynamics in regulating the stability of the phytoplankton community (Loreau and De Mazancourt 2008). We calculated the annual mean of community-wide species synchrony (ϕ_x) for each lake using the function: $\phi_x = \sigma^2 / (\sum_{i=1}^S \sigma_i^2)$, where ϕ_x is species synchrony, σ^2 is the temporal variance of community abundance, and σ_i is the standard deviation in the abundance of species i in a community with S species within each year. Species synchrony ranges between 0 (perfect asynchrony) and 1 (perfect synchrony). A negative association between species synchrony and community stability suggests that species asynchrony (that is, compensatory dynamics) promotes stability (Loreau and Mazancourt 2013).

All tested variables were *log* transformed before analyses to ensure normality and homogeneity. We used a linear mixed-effects model (LMM) to estimate the significance of slopes in the year trends for each variable, with lake nested within year as random factor. No significant patterns (all $P < 0.05$) were found in the residuals for LMMs subjected to year (1989–2008), suggesting that our

LMMs with random structures covered the temporal dependency.

We used two general approaches to discern the mechanisms influencing phytoplankton seasonal stability. Firstly, we applied LMMs to assess the relationships of seasonal stability, taxon richness, community dominance, synchrony, and community biomass and related each of these variables to nutrient resources (for example, TP and TN) and grazer richness and grazing pressure, with lake nested within year as random factor. Secondly, to get a more integrated map of the direct and indirect effects of nutrient resources and grazers on phytoplankton seasonal stability, we conducted a confirmatory path analysis based on piecewise fitting of LMMs components. The global-path model was nearly saturated in the sense that the component model for each endogenous variable included paths from all exogenous variables plus remaining endogenous variables, with the proviso that the model was non-recursive (that is, with no reciprocal paths between the same variables). Thus, our global models (Model 1) included several key hypothetical paths: (1) TP and TN as well as grazer richness and grazing pressure influence the taxon richness, community dominance, synchrony, community biomass, and seasonal stability of the phytoplankton community, (2) taxon richness, community dominance, and synchrony affect the community biomass and seasonal stability of the phytoplankton community, (3) community biomass affects the seasonal stability of the phytoplankton community. In addition, we included correlated error structures between taxon richness, synchrony and community dominance, TP and TN, grazer richness and grazing pressure, respectively, as no clear directions between them were hypothesized. The overall path model was evaluated using Shipley's test of directed separation, which yields a Fisher's C statistic that can be compared with a χ^2 -distribution. If the resulting P value is > 0.05 , then the model can be said to adequately reproduce the hypothesized causal network. Individual path coefficients leading to endogenous variables (that is variables with arrows leading to them) were fitted using restricted maximum likelihood (REML) and tested for significance. AICc procedure was applied to select the best SEM model (Shipley 2013). We used standardized path coefficients to present the direct, indirect, and total effects of the predictors (Grace and Bollen 2005).

As phytoplankton biomass might inherently be correlated with TP and TN, we also ran two alternative path models (Model 2 and Model 3) including different combinations of nutrient vari-

ables. Model 2 included only inorganic nutrients variables (PO_4 , NH_4 , NO_3) and Model 3 all available nutrients variables (TP, TN, PO_4 , NH_4 , NO_3) as well as water temperature and Secchi depth.

All statistical tests were performed using R version 3.51 software (Core 2013).

RESULTS

From 1989 to 2008, there was no clear pattern in the seasonal stability of phytoplankton communities between the studied lakes (Figure S1, Table S2) despite the occurrence of considerable long-term variations at individual lake scale (Figure S2). TP and TN as well as community biomass and dominance of phytoplankton decreased significantly, while grazer richness, grazing pressure, and phytoplankton taxon richness increased significantly after two decades of re-oligotrophication (Figure S1, Table S2). No significant patterns in species synchrony appeared over the years (Figure S1, Table S2).

The seasonal stability of the phytoplankton was positively associated with phytoplankton taxon richness ($Slope = 0.15$, $t = 3.62$, $P < 0.001$), and with grazer richness ($Slope = 0.28$, $t = 4.06$, $P < 0.001$) and grazing pressure ($Slope = 0.14$, $t = 6.45$, $P < 0.001$) (Figure 1) and negatively associated with synchrony ($Slope = -0.55$, $t = -29.54$, $P < 0.001$), community dominance ($Slope = -0.18$, $t = -9.23$, $P < 0.001$), and community biomass ($Slope = -0.18$, $t = -7.57$, $P < 0.001$) (Figure 2). However, TN, phytoplankton taxon richness and community biomass, as well as grazer richness and grazing pressure were not significant whereas TP was significant in determining the seasonal stability of phytoplankton when the linear mixed models included all the tested predictors (Table 1). This indicates that potentially confounding relationships among predictors may exist. Phytoplankton taxon richness decreased with TP ($Slope = -0.13$, $t = -4.06$, $P < 0.001$) and TN ($Slope = -0.14$, $t = -3.24$, $P = 0.001$) (Figure 3) and increased with grazer richness ($Slope = 0.51$, $t = 7.72$, $P < 0.001$) (Figure 4). Synchrony of phytoplankton decreased with grazer richness ($Slope = -0.43$, $t = -4.40$, $P < 0.001$) and grazing pressure ($Slope = -0.30$, $t = -0.98$, $P < 0.001$) (Figure 4). Community biomass and dominance of phytoplankton increased with TP ($Slope = 0.67$, $t = 11.47$, $P < 0.001$ and $Slope = 0.80$, $t = 11.79$, $P < 0.001$) and TN ($Slope = 0.65$, $t = 7.41$, $P < 0.001$ and $Slope = 0.75$, $t = 7.12$, $P < 0.001$) (Figure 3) and decreased with grazer richness ($Slope = -0.54$, $t = -4.46$, $P < 0.001$ and $Slope = -0.70$, $t = -4.88$, $P < 0.001$) and grazing

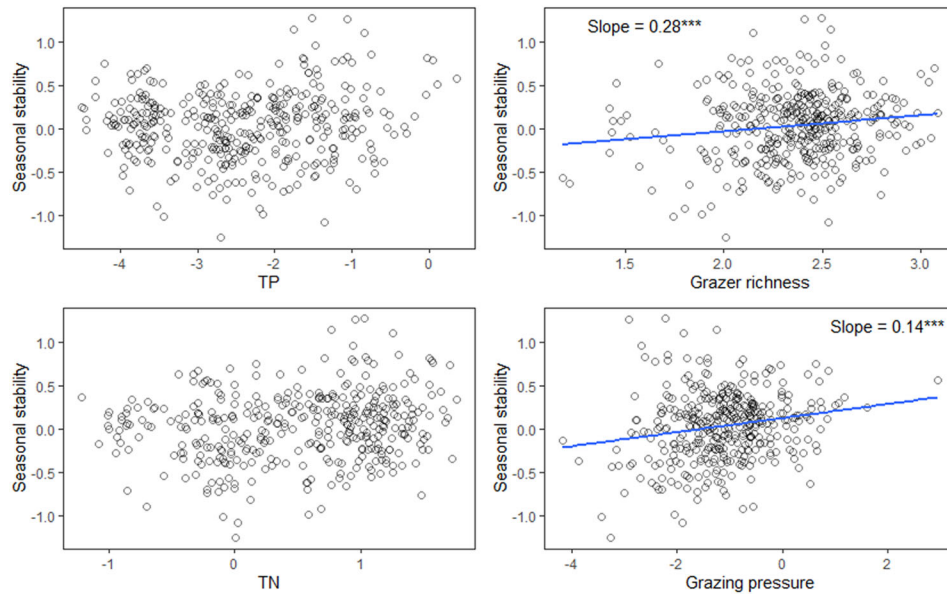


Figure 1. Effects of total phosphorus (TP, mg L^{-1}), total nitrogen (TN, mg L^{-1}), and grazer richness (zooplankton taxon richness, Number) and grazing pressure (biomass ratio of zooplankton:phytoplankton) on the seasonal stability of phytoplankton communities in 20 Danish lakes over two decades of re-oligotrophication (1989–2008). All variables were \log -transformed. Each point represents the annual mean values of each variable in each lake. The regression line is drawn in blue and statistic results are shown when significant. *** $P < 0.001$.

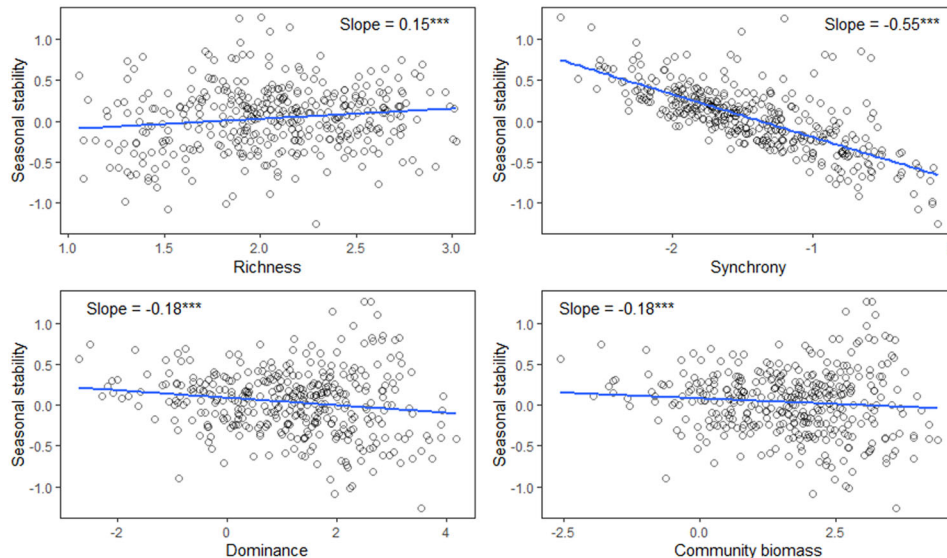


Figure 2. Effects of richness, synchrony, community dominance, and community biomass on the seasonal stability of phytoplankton communities in 20 Danish lakes over two decades of re-oligotrophication (1989–2008). All variables were \log -transformed. Each point represents the annual mean values of each variable in each lake. The regression line is drawn in blue and statistic results are shown when significant. *** $P < 0.001$.

pressure ($Slope = -0.64$, $t = -26.11$, $P < 0.001$ and $Slope = -0.75$, $t = -23.66$, $P < 0.001$) (Figure 4). However, TP was not significant in determining the taxon richness and synchrony of phytoplankton, and grazer richness was not significant in determining the community biomass

and dominance of phytoplankton when the linear mixed models included all the tested predictors (Table 2).

The accepted path model (Figure 5, Model 1: $\chi^2 = 11.54$, $d.f. = 12$, $P = 0.48$) explained 98% of the variation in the annual mean of community bio-

Table 1. Results of Linear Mixed Effects Model Analysis of the Effects of Richness, Synchrony, Community Dominance, Community Biomass, Grazer Richness (Zooplankton Taxon Richness) and Grazing Pressure (Biomass Ratio of Zooplankton:Phytoplankton), Total Phosphorus (TP), and Total Nitrogen (TN) on the Seasonal Stability of Phytoplankton Communities with Lake Nested Within Year as Random Effects Structure

Variables	Slope	t-value	P-value
Richness	0.06	1.58	0.11
Synchrony	- 0.53	- 24.09	<0.001
Community dominance	- 0.12	- 2.19	0.03
Community biomass	0.09	1.46	0.14
Grazer richness	0.07	1.59	0.11
Grazing pressure	- 0.02	- 0.98	0.33
TP	0.07	3.12	<0.001
TN	- 0.01	- 0.39	0.70

Slope, t-value, and P-value of the analysis are shown.

mass and 87% of phytoplankton seasonal stability. However, Model 3 including all nutrient variables (TP, TN, PO₄, NH₄, NO₃) as well as water temper-

ature and Secchi depth and Model 2 including only inorganic nutrient variables (PO₄, NH₄, NO₃) only marginally or did not at all enhance the R² for the different response variables (Table S3). As the standardized coefficient for each significant path in the final model is the partial effects considering all other variables, the amount of variation of phytoplankton community biomass and other variables did not differ between Model 1 (with total nutrients) and Model 2 (with inorganic nutrients), which suggests that phytoplankton community biomass tracked changes in either total nutrients or inorganic nutrients in the similar patterns. Furthermore, Model 1 has the lowest AIC, yielding the best model. We, therefore, only present the Model 1 results in the following.

According to Model 1, community dominance (42.3%) was the strongest predictor of community biomass (Table 3), followed by grazing pressure (23.6%), TP (20.3%), TN (7.2%), taxon richness (3.1%), grazer richness (2.4%), and synchrony (1.4%). All the tested predictors, except for synchrony and grazing pressure, promote community biomass. TP increased the community biomass of phytoplankton either directly or indirectly through

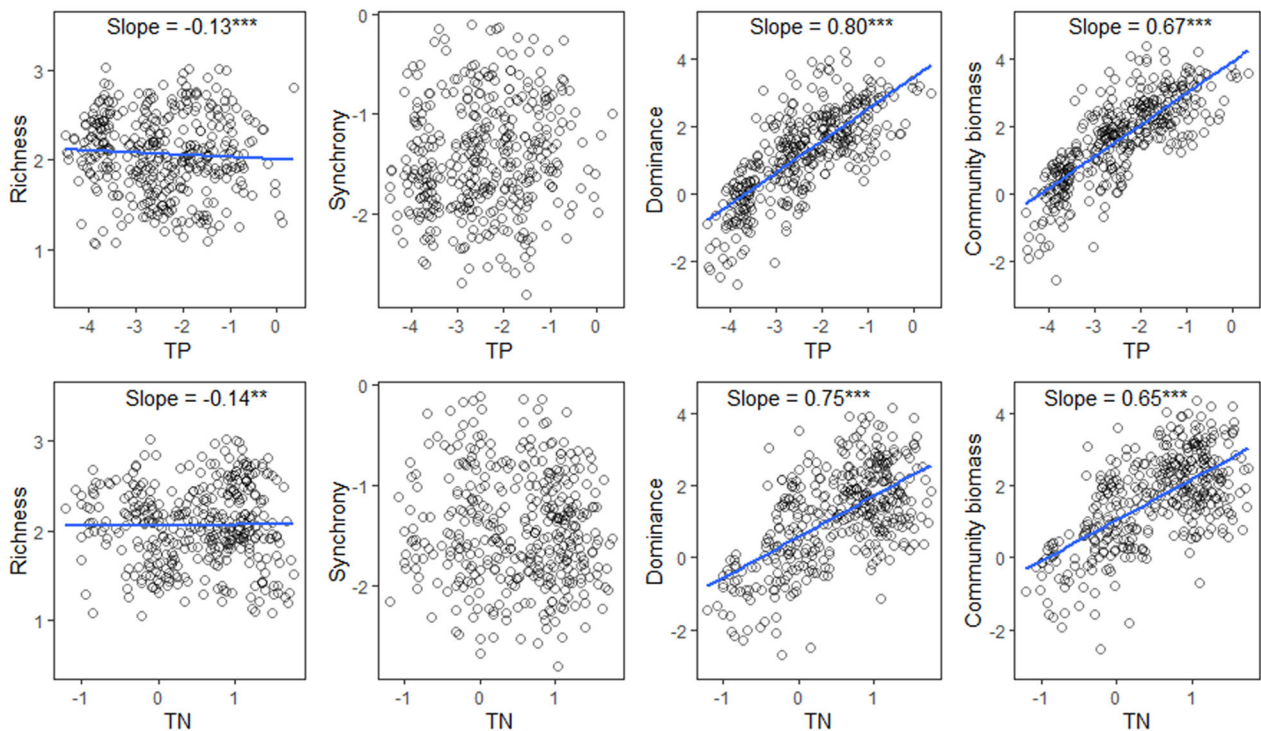


Figure 3. Effects of total phosphorus (TP, mg L⁻¹), total nitrogen (TN, mg L⁻¹) on the taxon richness, synchrony, community dominance, and community biomass of phytoplankton in 20 Danish lakes over two decades of reoligotrophication (1989–2008). All variables were *log*—transformed. Each point represents the annual mean values of each variable in each lake. The regression line is drawn in blue and statistic results are shown when significant. ***P* < 0.01, ****P* < 0.001.

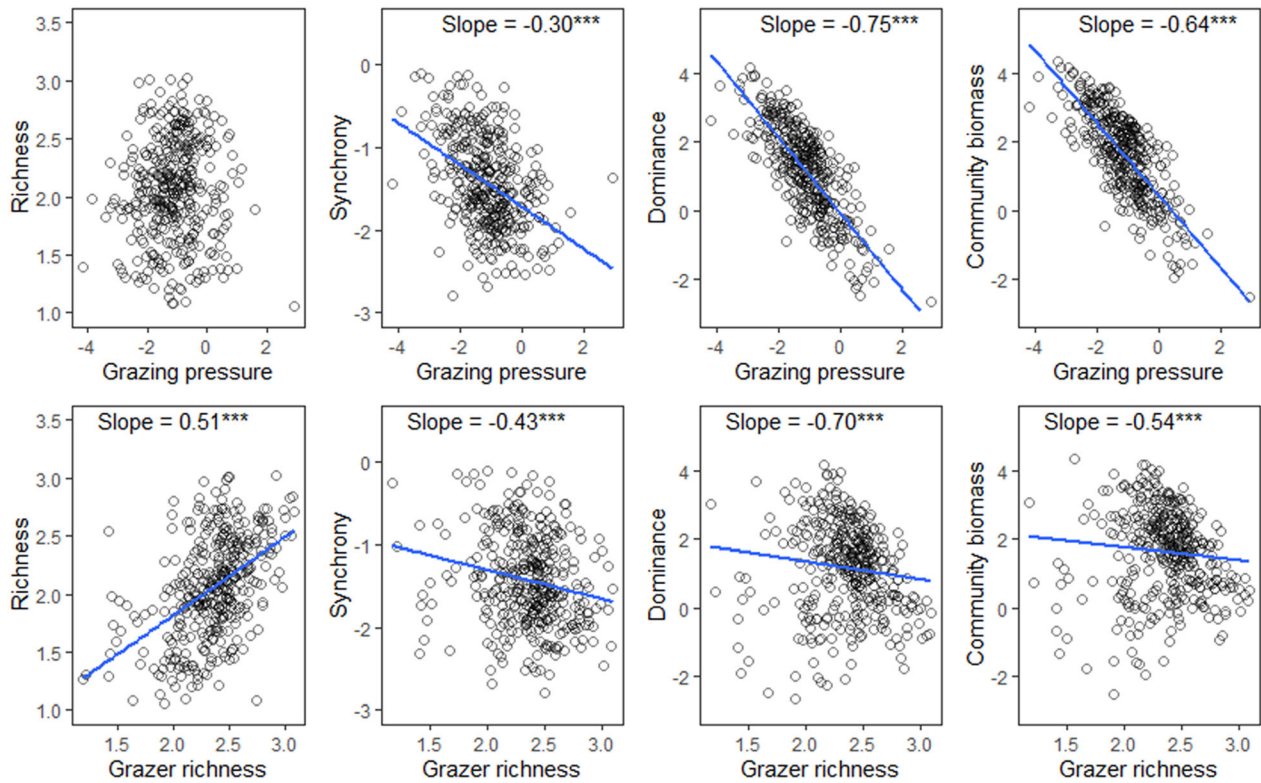


Figure 4. Effects of grazer richness (zooplankton taxon richness) and grazing pressure (biomass ratio of zooplankton:phytoplankton) on the taxon richness, synchrony, community dominance and community biomass of phytoplankton in 20 Danish lakes over two decades of re-oligotrophication (1989–2008). All variables were *log*—transformed. Each point represents the annual mean values of each variable in each lake. The regression line is drawn in blue and statistic results are shown when significant. ****P* < 0.001.

Table 2. Results of the Linear Mixed Effects Model Analysis of the Effects of Grazer Richness (Zooplankton Taxon Richness) and Grazing Pressure (Biomass Ratio of Zooplankton:Phytoplankton), Total Phosphorus (TP) and Total Nitrogen (TN) on the Richness, Synchrony, Community Dominance, and Community Biomass of Phytoplankton with Lake Nested Within Year as Random Effects Structure

Variables	Richness		Synchrony		Community dominance		Community biomass	
	Slope	<i>t</i> -value	Slope	<i>t</i> -value	Slope	<i>t</i> -value	Slope	<i>t</i> -value
Grazer richness	0.49	7.04***	− 0.24	− 2.57*	0.01	0.09	0.04	0.48
Grazing pressure	− 0.02	− 0.79	− 0.29	− 9.25***	− 0.68	− 21.92***	− 0.61	− 26.79***
TP	− 0.07	− 1.72φ	− 0.01	− 0.32	0.48	9.03***	0.45	11.57***
TN	− 0.09	− 1.91φ	− 0.12	− 2.03*	0.22	2.97**	0.15	3.06**

φ*P* < 0.1, **P* < 0.05, ***P* < 0.01, ****P* < 0.001. Slope, *t*-value and *P*-value of the analysis are shown.

changes in community dominance, whereas TN increased the community biomass of phytoplankton either directly or indirectly through changes in community dominance, taxon richness, and synchrony. Grazer richness promoted the seasonal stability of phytoplankton either directly or indirectly through changes in synchrony and richness,

while grazing pressure reduced the seasonal stability of phytoplankton either directly or indirectly through changes in synchrony and community dominance.

Synchrony (38.7%), followed by community dominance (20.6%), played a dominant role in destabilizing phytoplankton over the seasons (Ta-

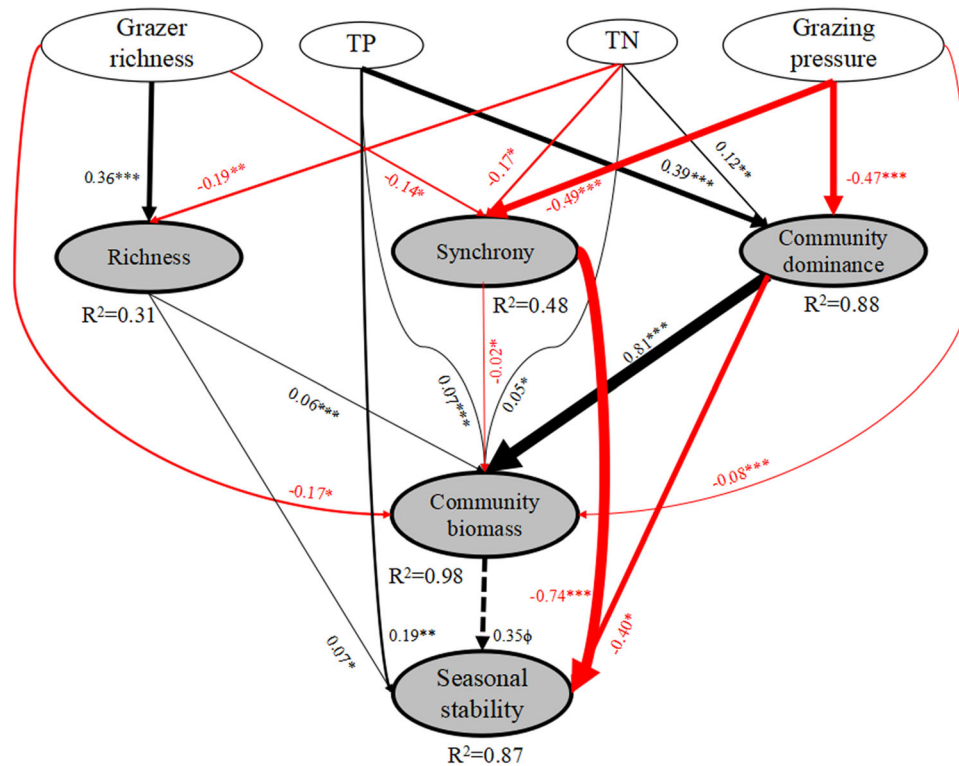


Figure 5. Confirmatory path analysis of the cascading effects of total phosphorus (TP) and total nitrogen (TN) and grazer richness (zooplankton taxon richness) and grazing pressure (biomass ratio of zooplankton:phytoplankton) on the seasonal stability of phytoplankton communities, encompassing direct and indirect effects through four biotic stabilizing pathways—richness, synchrony, community dominance, and community biomass. Arrows represent the flow of causality between TP and TN, grazer richness and pressure (first row of circles), biotic stabilizing pathways (second row of circles), community biomass (third row of circles), and seasonal stability of phytoplankton (fourth row of circles). We also correlated error structures between taxon richness, synchrony and community dominance, TP and TN, respectively. All variables were \log -transformed. This model provided the best fit to our data and was well supported ($\chi^2 = 4.96$, $d.f. = 4$, $P = 0.29$). Path coefficients (that is, numbers associated with each arrow) are standardized partial regression coefficients. Arrow width is proportional to the standardized path coefficients and can be interpreted as the relative importance of each factor. Dashed arrows represent marginally significant relationships, black arrows represent positive linear relationships, and red arrows represent negative linear relationships. The statistical significance for linear relationships was tested using likelihood-ratio tests. Component model R^2 (coefficient of determination) is shown in circles of response variables. All models contained random effects of lake nested within year. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; $\phi P < 0.1$.

ble 4). In contrast, taxon richness (3.4%) as well as TP (1.9%), TN (3.5%), and grazer richness (6.5%) and grazing pressure (28.9%) promoted the seasonal stability of phytoplankton (Figure 5, Table 3). TP had a direct effect on seasonal stability and also an important indirect effect via changes in community dominance. TN had an indirect effect on seasonal stability via three paths—changes in phytoplankton taxon richness, synchrony, and community dominance. Grazer richness had an indirect effect on seasonal stability via two paths—changes in phytoplankton taxon richness and synchrony. Grazing pressure had an indirect effect on seasonal stability via two paths—changes in synchrony and community dominance. Only a

marginal effect of community biomass on seasonal stability was observed. The path model also indicated that taxon richness was negatively correlated with community dominance (Path coefficients = -0.12 , $P < 0.009$) and synchrony (Path coefficients = -0.11 , $P < 0.014$), that synchrony was positively correlated with community dominance (Path coefficients = 0.40 , $P < 0.001$), that TP was positively correlated with TN (Path coefficients = 0.64 , $P < 0.001$), and that grazer richness was positively correlated with grazing pressure (Path coefficients = 0.11 , $P = 0.025$).

Table 3. The Pathways and Relative Contribution of All Candidate Predictors—Richness, Synchrony, Community Dominance, Community Biomass, Total Phosphorus (TP) and Total Nitrogen (TN), Grazer Richness (Zooplankton Taxon Richness) and Grazing Pressure (Biomass Ratio of Zooplankton:Phytoplankton)—to the Community Biomass of the Phytoplankton Community in the Final Path Model (Figure 1)

Predictors	Effects	Path codes	Pathways	Path coefficients	Total effects	Relative contribution (%)
Species synchrony (Syn)	Direct	Syn1		− 0.021	− 0.021	1.1
Community dominance (Dom)	Direct	Dom1		0.807	0.807	42.3
Species richness (Ric)	Direct	Ric1		0.059	0.059	3.1
TP	Direct	TP1		0.073	0.387	20.3
	Indirect	TP2	→ Dom1 →	0.314		
TN	Direct	TN1		0.053	0.138	7.2
	Indirect	TN2	→ Syn1 →	0.003		
	Indirect	TN3	→ Dom1 →	0.093		
	Indirect	TN4	→ Ric1 →	− 0.011		
Grazer richness (Gri)	Direct	Gri1		− 0.017	0.045	2.4
	Indirect	Gri2	→ Syn1 →	0.003		
	Indirect	Gri3	→ Ric1 →	0.059		
Grazing pressure (Gpr)	Direct	Gpr1		− 0.080	− 0.450	23.6
	Indirect	Gpr1	→ Syn1 →	0.010		
	Indirect	Gpr2	→ Dom1 →	− 0.380		

Path coefficients were calculated as the arithmetic product of coefficients of all paths in a particular direct or indirect pathway. Total effects were calculated as the sum of coefficients of all potential direct and indirect pathways.

Table 4. The Pathways and Relative Contribution of All Candidate Predictors—Richness, Synchrony, Community Dominance, Community Biomass, Grazer Richness (Zooplankton Taxon Richness) and Grazing Pressure (Biomass Ratio of Zooplankton:Phytoplankton), Total Phosphorus (TP), and Total Nitrogen (TN)—to the Seasonal Stability of Phytoplankton Communities in the Final Path Model (Figure 4)

Predictors	Effects	Path codes	Pathways	Path coefficients	Total effects	Relative contribution (%)
Species synchrony (Syn)	Direct	Syn1		− 0.743	− 0.743	38.7
Community dominance (Dom)	Direct	Dom1		− 0.396	− 0.396	20.6
Species richness (Ric)	Direct	Ric1		0.066	0.066	3.4
TP	Direct	TP1		0.190	0.036	1.9
	Indirect	TP2	→ Dom1 →	− 0.154		
TN	Indirect	TN1	→ Syn1 →	0.124	0.066	3.5
	Indirect	TN2	→ Dom1 →	− 0.046		
	Indirect	TN3	→ Ric1 →	− 0.012		
Grazer richness (Gri)	Indirect	Gri1	→ Syn1 →	0.102	0.126	6.5
	Indirect	Gri2	→ Ric1 →	0.024		
Grazing pressure (Gpr)	Indirect	Gpr1	→ Syn1 →	0.368	0.554	28.9
	Indirect	Gpr2	→ Dom1 →	0.187		

Path coefficients were calculated as the arithmetic product of the coefficients of all paths in a particular direct or indirect pathway. Total effects were calculated as the sum of coefficients of all potential direct and indirect pathways.

DISCUSSION

Using a two-decade data set on phytoplankton dynamics, we observed no significant long-term patterns in the seasonal stability of phytoplankton communities across lakes during re-oligotrophication (Figure S1). We used annual means of phytoplankton taxon richness, community biomass, and dominance as the three important predictors affecting seasonal stability (the ratio of annual mean biomass relative to temporal annual standard deviation for each year) of phytoplankton community. The three indexes are also the major proxies of the three biotic stabilizing mechanisms (portfolio, selection, and over-yielding). Instead of annual mean values of these indexes, other measures (for example, coefficient variations, standard deviation, skewness, and so on) could also be considered. However, our results have yielded 87% variations of phytoplankton seasonal stability, suggesting that annual means are effective in determining the seasonal stability of phytoplankton.

Among the four tested biotic stabilizing mechanisms, compensatory dynamics (as indicated by synchrony) led to increased seasonal stability in lakes with high TN and high grazer richness and grazing pressure, while the portfolio effect (as indicated by taxon richness) promoted seasonal stability in lakes with low TN and high grazer richness (Figure 5). However, strongly negative selection effects (as indicated by community dominance) were observed in lakes with high TP, high TN, as well as low grazing pressure, as suggested by a negative correlation between community dominance and seasonal stability. Our results thus provide evidence that biotic mechanisms vary in importance in maintaining the seasonal stability of phytoplankton communities along nutrient concentration and grazer dynamics gradients.

The most important pathway by which water nutrients (TP and TN) and grazer richness and grazing pressure affected phytoplankton seasonal stability was via species synchrony (Figure 5). For the pathways impacted by nutrients, lakes with high TN and high TP (reflected by the strong positive correlation between TN and TP in the final path model) elicited a weak synchronous response among taxa and, thus, high taxa asynchrony related to increased community biomass and seasonal stability of phytoplankton. We interpret this relationship as evidence of an increasing importance of compensatory dynamics with increasing TN and TP. In many case studies, phytoplankton taxa have shown significantly different phenology shifts as

well as plasticity in the seasonal succession during lake re-oligotrophication (Anneville and others 2004; Anneville and others 2005; Thackeray and others 2008; Anneville and others 2018), implying that temporal niche complementary effects (compensatory dynamics) occur over the seasons. However, previous findings of the strength of compensatory dynamics along a nutrient gradient remain debatable. Supporting our findings, significant compensatory dynamics occurred only in the nutrient-enriched state with high phytoplankton biomass in Lake Constance, Germany, while being less pronounced in the oligotrophic state (Jochimsen and others 2013). Likewise, increased importance of compensatory dynamics under N-enriched conditions was observed in an *in situ* grassland experiment where stronger compensatory dynamics contributed to the stability of fertilized communities (Emily and others 2010). In highly eutrophic lakes, biomass decreases of sensitive taxa or functional groups were offset, though, by increases in the population growth of high nutrient tolerant taxa over the seasons (Reynolds 1984). Our results provide further evidence that the influence of compensatory dynamics in determining the seasonal stability of natural phytoplankton communities become stronger when nutrient levels are high.

Our results are in contrast to recent findings from a microcosms study showing strong compensatory dynamics of six phytoplankton species at low nutrient availability in which all chambers experienced lowered temperature from 25 to 18 °C during the study period (Zhang and Zhang 2006), indicating that the experimental algal communities grown under low nutrient conditions were resistant to temperature perturbation due to asynchronous responses of different species to environmental fluctuations. The difference between these results and ours might reflect the much more functionally diverse phytoplankton communities found in natural ecosystems than in the Zhang and Zhang (2006) experiment (as only six phytoplankton species were involved), triggering a more diverse response of phytoplankton to nutrients. In addition, the strength of compensatory dynamics of a phytoplankton community might depend not only on the nutrients but also on the studied temporal scale (Anderson and others 2019). In contrast to our findings of marked compensatory dynamics of phytoplankton at a seasonal scale, Zhang and others (2018) did not find strong compensatory dynamics of phytoplankton groups at an annual scale in Lake Taihu, a highly eutrophic shallow lake in China undergoing decades of

eutrophication. Indeed, Vasseur and Gaedke (2007) found scale dependency of compensatory dynamics of phytoplankton communities, mainly at sub-annual scale, leading to a substantial reduction of community-level variability.

We found that lakes with high grazer richness and grazing pressure were associated with decreasing synchrony among phytoplankton taxa, that is high taxa asynchrony led to increased community biomass and seasonal stability of the phytoplankton (Figure 5, Table 4). High grazer richness might entail great diversity of grazer functional groups (for example, body size), which may increase the importance of compensatory dynamics for the stability of phytoplankton communities (Özkan and others 2014). For example, large grazers may suppress the growth of some groups of phytoplankton, whereas others could be relieved from competition and thereby compensate for the loss of community biomass, thereby having a stabilizing effect on community biomass over the seasons. Compensatory dynamics have previously been demonstrated between edible and less-edible functional groups in Lake Constance at high grazing pressure during the growing season (Vasseur and others 2005). In a mesocosm experiment manipulating copepod and cladoceran biomass, Sommer and others (2001) found a complementary impact of grazers on phytoplankton, producing compensatory dynamics among small and large phytoplankton groups. Moreover, a high grazing pressure creates refuges for less competitive phytoplankton taxa or groups, which reduces exclusion and improves the compensatory dynamics for the seasonal succession of phytoplankton communities (Proulx and others 2012). Our results thus provide further support for the view that altering grazer diversity and abundance may affect the stability of phytoplankton communities to nutrient perturbations (Cottingham and Schindler 2000).

The portfolio effect, although relatively weak (3.4%), was the second biotic mechanism mediating effects of nutrients and grazers on the seasonal stability of phytoplankton (Figure 5, Table 4). Lakes with low TN allow more species to coexist, and high species richness promotes seasonal stability. This is in accordance with the results from a nutrient enrichment experiment conducted by Zhang and Zhang (2006) with six green algal species, suggesting a stronger stabilizing effect of richness in a nutrient-poor environment than under nutrient-enriched conditions. Our previous results also indicated a significant decrease of TP and TN in the most meso- to hypertrophic lakes, with incidental increases in the taxon richness of

phytoplankton and zooplankton during re-oligotrophication (Özkan and others 2014, 2016). In addition, our results suggest that increases in zooplankton richness lead to increases in phytoplankton richness, which is consistent with previous findings of strong congruence in community composition between zooplankton and phytoplankton in a subset of the studied lakes (Özkan and others 2014). The path model results indicated that the taxon richness of phytoplankton had a weak effect (3.1%) on phytoplankton biomass and was negatively associated with community dominance and synchrony (Table 4), both findings indicating that negative selection effects as well as positive compensatory dynamics under nutrient-enriched condition had a significant diversity effect on the seasonal stability of the phytoplankton communities.

In contrast to the expectation that increasing community dominance would increase stability (Lehman and Tilman 2000), we found that greater community dominance decreased the seasonal stability of phytoplankton communities at high nutrient concentrations and low grazing pressure despite its important role in promoting the community biomass of phytoplankton (Figure 5). Our results identified an opposite pattern of selection effects on the community biomass (positive) and seasonal stability (negative) of phytoplankton. The positive selection effect on community biomass could, in part, reflect released growth and reproduction of phytoplankton under nutrient-enriched conditions as well as higher fish predation on zooplankton (Jeppesen and others 2002), resulting in a low zooplankton:phytoplankton biomass ratio (that is, low grazing pressure). However, the observed negative selection effect contrasts with results from a mesocosm experiment where enhanced stability of the phytoplankton community was observed with increasing density of the large colonial cyanobacterium *Gloeotrichia echinulate* (Carey and others 2017). The significant shifts in dominant taxa over seasons might have a destabilizing effect on population dynamics and, thus, the phytoplankton community. Furthermore, previous studies conducted in Lake Constance suggest that synchronous dynamics predominate among the dominant populations in plankton communities (Vasseur and Gaedke 2007), thereby increasing the temporal variability of phytoplankton community biomass. In our study, the path model demonstrated a strong positive correlation between community dominance and species synchrony (Figure 5). These results imply that the higher the community dominance is, the more synchronous

are the responses of phytoplankton species to their environments, lending further support to the observed negative selection effects on the seasonal stability of phytoplankton communities.

Besides its negative effects through community dominance, TP could also directly promote the seasonal stability of phytoplankton communities and thus have a weak positive effect (Table 4). This suggests that phytoplankton can track the changes in TP not only at the taxon level but also at the community level. High TP under year-round P-enriched conditions might have a stabilizing effect on the seasonal succession of phytoplankton communities. Our results also indicated that the strong compensatory effects at high nutrient levels as well as the portfolio effects at low nutrient levels are offset by the negative selection effects, resulting in a relatively weak stabilizing effect of TN. Surprisingly, the total effects of grazer richness and grazing pressure (35.4%) were much higher than those of TP and TN (5.3%) (Table 4), which might be explained by the decreasingly negative selection effects at higher grazer richness and grazing pressure at higher nutrient concentrations.

In conclusion, our results suggest that compensatory dynamics increased the importance of promoting the seasonal stability of phytoplankton at high nutrient and high grazer richness and grazing pressure, whereas the portfolio effect was a more important promoting factor at low TN and high grazer richness. We also found positive selection effects on community biomass and negative selection effects on seasonal stability of phytoplankton. The strong destabilizing effect of community dominance was counteracted by the combined stabilization of compensatory dynamics and/or portfolio effects at high nutrient levels. The shifts in the importance of the different potential stability mechanisms subjected to nutrient and grazer control may help explain why the seasonal stability of phytoplankton communities varies among lakes during re-oligotrophication. Overall, top-down forces were more important than bottom-up forces in determining the seasonal stability of the phytoplankton communities in the study lakes. Therefore, our study indicates that the phytoplankton community can maintain a seasonally stable biomass through a variety of biotic mechanisms in response to both changes in nutrients and grazers communities despite marked shifts in the taxon richness and composition of the phytoplankton. With nutrient loading reduction, we can expect an increase in the role of top-down control on phytoplankton (higher zooplankton:phytoplankton ratio with less fish predation on zoo-

plankton) (Jeppesen and others 2011), whereas climate warming may have the opposite effect due to increasing predation on zooplankton (Meerhoff and others 2012).

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DATA AVAILABILITY

Data are from the national survey program and can be obtained from <https://danmarksmiljoportal.zendesks.com/hc/da>.

Compliance with Ethical Standards

Conflict of interest The authors declare no competing financial interests.

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