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Lake browning counteracts cyanobacteria responses to nutrients: Evidence from phytoplankton dynamics in large enclosure experiments and comprehensive observational data

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Abstract

Lakes worldwide are affected by multiple stressors, including climate change. This includes massive loading of both nutrients and humic substances to lakes during extreme weather events, which also may disrupt thermal stratification. Since multi-stressor effects vary widely in space and time, their combined ecological impacts remain difficult to predict. Therefore, we combined two consecutive large enclosure experiments with a comprehensive time-series and a broad-scale field survey to unravel the combined effects of storm-induced lake browning, nutrient enrichment and deep mixing on phytoplankton communities, focusing particularly on potentially toxic cyanobacterial blooms. The experimental results revealed that browning counteracted the stimulating effect of nutrients on phytoplankton and caused a shift from phototrophic cyanobacteria and chlorophytes to mixotrophic cryptophytes. Light limitation by browning was identified as the likely mechanism underlying this response. Deep-mixing increased microcystin concentrations in clear nutrient-enriched enclosures, caused by upwelling of a metalimnetic *Planktothrix rubescens* population. Monitoring

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data from a 25-year time-series of a eutrophic lake and from 588 northern European lakes corroborate the experimental results: Browning suppresses cyanobacteria in terms of both biovolume and proportion of the total phytoplankton biovolume. Both the experimental and observational results indicated a lower total phosphorus threshold for cyanobacterial bloom development in clearwater lakes ($10–20\,\mu g\,P\,L^{-1}$) than in humic lakes ($20–30\,\mu g\,P\,L^{-1}$). This finding provides management guidance for lakes receiving more nutrients and humic substances due to more frequent extreme weather events.

KEYWORDS
climate change, deep-mixing, harmful algal blooms, lake browning, large-scale lake survey, long-term monitoring, mesocosm, multiple stressors, nutrient gradient

1 | INTRODUCTION

Multiple stressors, such as nutrient enrichment and climate change have increased the occurrence of cyanobacterial blooms in lakes worldwide (Huisman et al., 2018), posing severe challenges for lake management (Jeppesen et al., 2017). Nutrient enrichment from diffuse agricultural runoff and urban wastewater is the reason for moderate or worse ecological status in 22% of lakes in the EU and Norway, ranging from <20% in northern countries to >60% in many Central European countries (EEA, 2018). Nutrient inputs causing toxic cyanobacterial blooms threaten ecosystem services such as safe drinking and bathing water (Carvalho et al., 2013; Chorus & Welker, 2021; Huisman et al., 2018). The responses of lakes to nutrient enrichment are highly variable, depending on a range of characteristics including basin morphometry, retention time, alkalinity, humic substances and food-web structure (Phillips et al., 2013; Ptacnik et al., 2008; Woolway et al., 2020).

During the last two decades, the concentration of colored dissolved organic matter (cDOM) in lakes has increased over large areas, causing browning of the lake water, particularly in boreal catchments, due to a combination of reduced rainwater acidity and climate change entailing increased rainfall and runoff including humic substances (de Wit et al., 2016; Meyer-Jacob et al., 2019). Browning is not limited to softwaters but can also occur in hardwater lakes, triggering regime shifts with consequences for ecosystem structure and functioning (Brothers et al., 2014; Williamson et al., 2015). Differences in responses to nutrients can be partly attributed to browning (Isles et al., 2021; Vuorio et al., 2020), which reduces underwater irradiance due to light absorption by cDOM. Moreover, the light spectrum is shifted towards the red spectral range of photosynthetically active radiation (PAR, 400–700 nm), because cDOM preferentially absorbs light in the blue range (Falkowski & Raven, 2013).

Altered light conditions modify competitive interactions of phytoplankton species (Lebret, Langenheder, et al., 2018; Luimstra et al., 2020; Stomp et al., 2007). Shade-tolerant cyanobacteria (e.g., *Planktothrix rubescens* and *Aphanizomenon flos-aquae*) tend to dominate at low light levels, for instance when forming a deep chlorophyll

maximum (DCM; Selmeczy et al., 2016; Smith, 1986). Other cyanobacteria, however, are more successful at high light intensities (e.g., *Microcystis aeruginosa*; Muhetaer et al., 2020; Oliver & Ganf, 2000). The ability to move vertically in stratified water columns by means of gas vacuoles enhances the flexibility of cyanobacteria to cope with poor light conditions, whether in terms of irradiance or spectral composition (Reinl et al., 2021). Other phytoplankton species such as cryptophytes are also highly mobile and can cope with poor light conditions by combining photosynthesis and phagotrophy due to their mixotrophic abilities (Mitra et al., 2016). Both cyanobacteria and cryptophytes have phycobiliproteins as accessory pigments, which absorb blue-green, green or orange light (Cunningham et al., 2019; Falkowski & Raven, 2013). This feature provides the two taxonomic groups an additional competitive advantage in lakes affected by browning, when pH and alkalinity are sufficiently high to ensure adequate bicarbonate (HCO_3^-) supply for photosynthesis (Senar et al., 2021).

Forecasts of climate change impacts on lake ecosystems must incorporate extreme weather events, such as summer storms, which are predicted to become more frequent (Gastineau & Soden, 2009; IPCC, 2021; Jennings et al., 2012; Stockwell et al., 2020). Such events cause large loads of nutrients and cDOM from the catchment to lakes, adding to any long-term trends (de Wit et al., 2016). Risk of blooms can also be exacerbated in nearshore waters of large oligotrophic lakes following increased nutrient loading after extreme rainfall (Sterner, Keeler, et al., 2020; Thrane et al., 2022). Additionally, severe storms may disrupt the thermal stratification of lakes by inducing deep mixing (Kasprzak et al., 2017; Kuha et al., 2016). The consequences vary with storm intensity and frequency and also with characteristics of the affected lake (Doubek et al., 2021; Jennings et al., 2012; Stockwell et al., 2020). Filamentous cyanobacteria tend to be disfavored by storm-induced turbulence and deep mixing (Moe et al., 2019; Visser et al., 2016). However, when mixing redistributes populations initially concentrated in a DCM, blooms of cyanobacteria can develop within the surface layer of stratified lakes, driven by enhanced availability of light and nutrients (Giling et al., 2017, 2020; Kasprzak et al., 2017).

Unravelling the complex interplay between these multiple stressors remains an important challenge for understanding and assessing their combined impacts on phytoplankton communities, including risks of harmful algal blooms and adapt lake management strategies accordingly (Carvalho et al., 2013; Côté et al., 2016). All three drivers can be induced by storms and heavy rain events, in addition to gradual browning and nutrient enrichment over time. We hypothesized that browning counteracts the effects of nutrient enrichment on phytoplankton due to the blocking of incident light by cDOM, which limits phytoplankton growth and changes species composition. Furthermore, we expected that deep mixing induces cyanobacterial blooms in the epilimnion, when a metalimnetic bloom (DCM) exists prior to deep mixing, unless light limitation is severe because of browning. We tested these hypotheses by combining two consecutive enclosure experiments with a comprehensive time-series and a broad spatial-scale lake dataset to evaluate the responses of phytoplankton communities in stratified lakes to nutrient enrichment, browning, and deep mixing disrupting the thermocline. Our main goals were (i) to determine the combined effects of browning and nutrient enrichment on phytoplankton communities with particular attention to harmful cyanobacteria, (ii) to investigate how storm-induced deep mixing interacts with nutrient enrichment and browning to affect phytoplankton communities, and (iii) to provide guidance to improve nutrient management strategies for stratifying lakes.

## 2 | MATERIALS AND METHODS

2.1 | Research approach

Our research approach covers three complementary approaches (Figure 1): (a) two consecutive large enclosure experiments in the LakeLab installed in Lake Stechlin (North-Eastern Germany) applying gradients of nutrient loading and browning combined with deep mixing to assess the combined effects on natural plankton communities, (b) a 25-year time-series from Lake Vansjø-Vanemfjorden (South-Eastern Norway) analyzing the dynamics of nutrients and browning over time, (c) a large lake dataset including nearly 600 lakes across northern Europe covering long gradients of nutrients and browning (Moe et al., 2013). Comparing these three lines of evidence is crucial to elucidate the generality of combined stressor effects on phytoplankton communities in experimental and natural lake ecosystems.

2.2 | Enclosure experiments

2.2.1 | Set-up and experimental design

Two consecutive enclosure experiments were carried out in summer 2015 at the LakeLab, a large enclosure facility deployed in the deep stratified clear-water Lake Stechlin (North-Eastern Germany, Figure 1a). We used a total of 21 enclosures, each ca. 20 m deep and 9 m in diameter, thereby enclosing a water volume of ca. 1300 m^3 (Giling et al., 2017). A gradient design was chosen to maximize the number of predictor levels, instead of replication at each level (Bergström & Karlsson, 2019; Gerhard et al., 2023; Kreyling et al., 2018). This design is well suited to capture non-linear responses of phytoplankton and cyanobacteria to nutrient enrichment (Carvalho et al., 2013; Ptacnik et al., 2008).

Experiment I was designed to test for effects of a single heavy rain event by simulating one major initial pulse of nutrients and browning. Seven nutrient levels were fully crossed with three browning levels (Table 1a). The intended concentrations of total phosphorus (TP) covered a broad gradient from oligo-mesotrophic to eutrophic conditions (Table 1a) including the critical threshold for cyanobacteria response to nutrient enrichment (Carvalho et al., 2013). An arithmetic progression ($a_n = 18 + n^2$) was applied to select the intended TP concentrations, starting with the lake epilimnion TP (18 μg L^{-1}). Phosphorus (P) and nitrogen (N) were added as orthophosphoric acid (H_3PO_4) and ammoniumnitrate (NH_4NO_3). Nitrogen was added
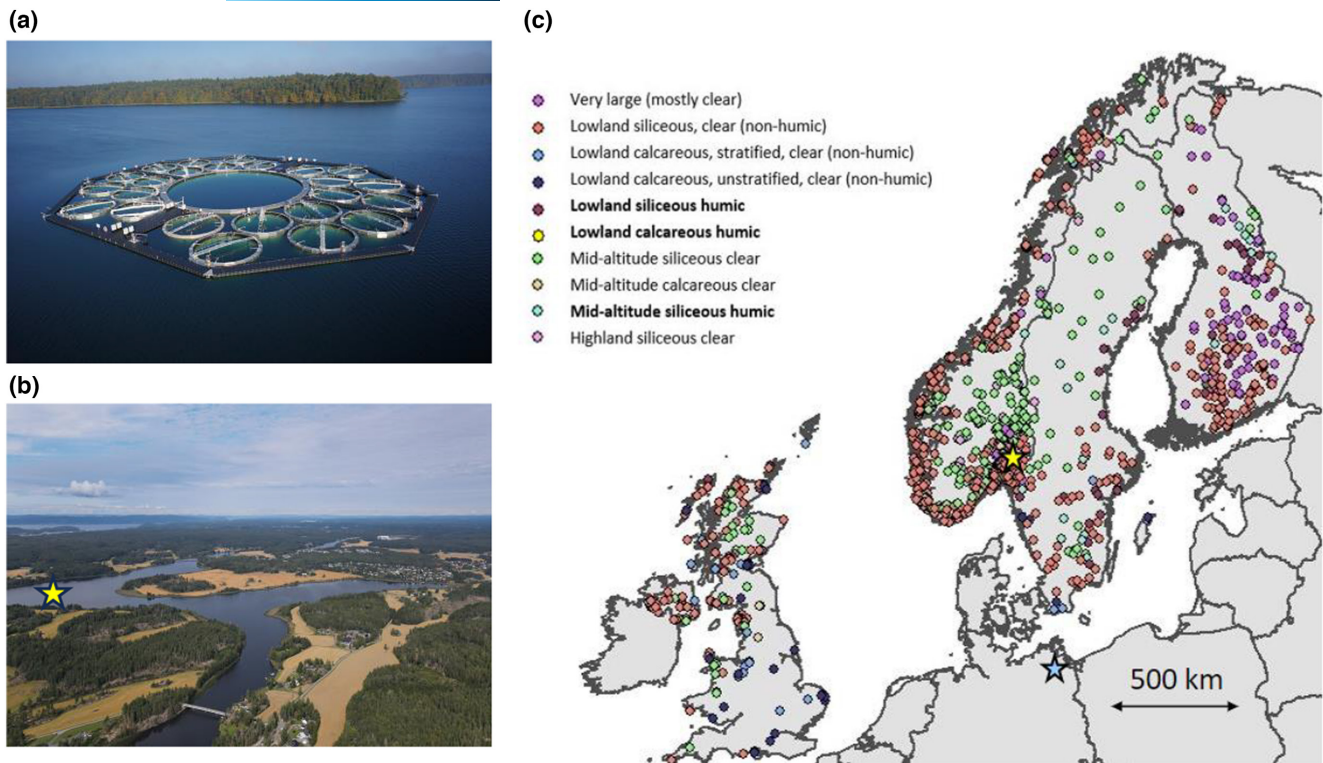
FIGURE 1 The three approaches of the study: (a) Large experimental enclosure facility (LakeLab) installed in Lake Stechlin, North-Eastern Germany (photo M. Oczipka, HTW Dresden/IGB Berlin), each enclosure has a diameter of 9 m; (b) Long-term monitoring site in the Vanemfjorden basin (surface area of 11.4 km²) of Lake Vansjø, South-Eastern Norway (photo Unum Media kindly provided by the river basin manager Carina Rossebø Isdahl), and (c) Location of 588 lake monitoring sites in northern Europe with colors indicating different lake types (see legend, humic lake types in bold font). Map lines delineate study areas and do not necessarily depict accepted national boundaries. The blue star shows the location and lake type of the LakeLab photo in North-Eastern Germany and the yellow star shows the location and type of the Lake Vansjø-Vanemfjorden basin photo in South-Eastern Norway.

to ensure a ratio of bioavailable N to P as in the lake water, which was close to the Redfield ratio (7:1 by mass). Browning was achieved by adding HuminFeed (HF; HuminTech GmbH, Grevenbroich, Germany), a highly soluble natural commercial product that has the advantage of strongly staining water without adding significant amounts of bioavailable carbon or nutrients (Scharnweber et al., 2021). Three browning levels corresponded to browning levels in natural lakes: (A) low=clear or oligohumic (<5 mg Pt L⁻¹, no addition of HF); (B) medium=mesohumic (67 mg Pt L⁻¹, addition of 5 mg HF L⁻¹); (C) high=polyhumic (133 mg Pt L⁻¹, addition of 10 mg HF L⁻¹). Experiment I lasted 7 weeks from early June to late July 2015. The amounts of HF, P, and N added to each enclosure are given in Table S1.

Experiment II followed directly after the end of Experiment I without changing the water in the enclosures and lasted for 7 weeks from late July to early September 2015. This experiment was designed to test for effects of repeated nutrient enrichment and browning by weekly adding nutrients and humic substances, as well as physically disrupting the thermocline by deep mixing, thus simulating a series of storm events. Nutrients and HF were added for 7 weeks following the scheme shown in Table 1b. For each enclosure, the amounts of added nutrients and HF were the same each week after initially adjusting the concentrations to the intended level (Table 1b). The added amounts differed among the enclosures to ensure a relatively

constant nutrient enrichment level for each of them (Table S1). Nine of the 21 enclosures used in the experiment (three for each browning level) were weekly mixed to 14 m depth referred to as deep-mixed (dm; Table 1b), while avoiding sediment disturbance (Section S1.1). Mixing of the 12 remaining enclosures, which served as controls for the deep-mixing treatments, was limited to 8 m depth referred to as shallow-mixed (sm; Table 1b), reflecting the epilimnion depth of Lake Stechlin between 7 and 9 m. The amounts of nutrients added were calculated to obtain the same phosphorus concentrations for both mixing treatments (15=no addition, 20, 30 and 50 μg P L⁻¹) and the three browning levels. Target concentrations for the browning were <5 (no HF addition), 30 and 60 mg Pt L⁻¹ (addition of 2.25 and 4.5 mg HF L⁻¹) for the medium and high browning levels, respectively.

2.2.2 | *In situ* measurements, sampling, and analyses

All enclosures were equipped with automatic profilers holding multiparameter probes for continuous measurements of water temperature, pH, oxygen, turbidity, and chlorophyll fluorescence (YSI Inc., Yellow-Springs, USA; see further details in Section S1.1) and sensors to measure PAR (LI-193 Spherical Underwater Quantum Sensor, LI-COR Inc., Lincoln, NE, USA). PAR, blue, green, and red light were also

TABLE 1 Designs of Experiments I and II conducted in 21 enclosures (A1-C7) deployed in a stratified clearwater lake. (a) Experiment I (single nutrient and browning pulse) ran from 10th June to 28th July 2015 and involved seven nutrient and three browning levels. (b) Experiment II ran from 28th July to 8th September 2015 and involved four nutrient and three browning levels in addition to deep vs. shallow mixing (weekly additions of nutrients and HF and weekly deepening of the thermocline for 7 weeks). All values are nominal concentrations.

(a) Experiment I		Intended initial TP concentrations ($\mu g\,L^{-1}$)						
Browning	Color ($mg\,Pt\,L^{-1}$)	18	19	22	27	34	43	54
Low (clear)	<5	A1	A2	A3	A4	A5	A6	A7
Medium	67	B1	B2	B3	B4	B5	B6	B7
High	133	C1	C2	C3	C4	C5	C6	C7

(b) Experiment II			Intended levels of TP concentrations ($\mu g\,L^{-1}$)			
Mixing treatment	Browning	Color ($mg\,Pt\,L^{-1}$)	15	20	30	50
Shallow mixed	Low (clear)	5	A1	A2	A4	A6
Deep mixed	Low (clear)	5	–	A3	A5	A7
Shallow mixed	Medium	30	B1	B2	B4	B6
Deep mixed	Medium	30	–	B3	B5	B7
Shallow mixed	High	60	C1	C2	C4	C6
Deep mixed	High	60	–	C3	C5	C7

measured weekly with a spectroradiometer from the surface down to the euphotic depth during Experiment I (Section S3). Secchi depth was recorded weekly with a 30-cm diameter white disc. Epilimnion depth in the enclosures was derived from temperature profiles in the enclosures, which were the same as in the surrounding lake (Berger et al., 2006). Epilimnion depth ranged from 6.5 to 7 m. In Experiment II, the epilimnion depth in the lake increased to 7–9 m, and was experimentally increased weekly to 14 m in the deep-mixed enclosures.

A hose sampler was used to take weekly integrated water samples from the epilimnion (Section S1.1). The sampling depth was adjusted weekly in line with the epilimnion depth measured on each sampling day. The water samples were filled in 20-L carboys and transported to the laboratory within 30 min after collection, where subsamples were immediately taken for analyses of water color (absorbance at 436 nm converted to $mg\,Pt\,L^{-1}$), concentrations of dissolved organic carbon (DOC), total phosphorus (TP), soluble reactive phosphorus (SRP), total nitrogen (TN), ammonium (NH_4^+), nitrate (NO_3^-) and nitrite (NO_2^-) and chlorophyll *a* (Section S1.2, Table S2). Subsamples of 250 mL were preserved with acid Lugol's solution for determination of community composition and total phytoplankton biovolume (Section S1.3). Cyanotoxins were analyzed with ELISA kits on epilimnetic samples that were stored frozen (–20°C) until analysis (Section S1.3). Mesozooplankton was sampled weekly by taking vertical hauls from 1.5 m above the sediment to the surface using a 90-μm mesh plankton net and analyzed as described in Section S1.4. The zooplankton:phytoplankton carbon ratio was used to indicate the level of zooplankton grazing (Jeppesen et al., 2011).

2.2.3 | Dataset from both experiments

The dataset from the experiments which have been used for this paper has been published by Berger et al. (2023).

2.3 | Time-series data from Lake Vansjø, Norway

Lake Vansjø is a stratified lowland lake (37 km²) in South-Eastern Norway, located in a 690 km² catchment dominated by mixed deciduous and coniferous forest with some agricultural areas; the lake is extensively used for recreational activities (Moe et al., 2019). The lake consists of two basins, Storefjorden, the eastern large, oligo-mesotrophic basin (23.7 km²) with low alkalinity (0.2 mM L⁻¹) and a mean depth of 9 m, and Vanemfjorden, the western smaller (11.4 km²) and shallower (mean depth of 4 m), but still stratified basin, which is meso-eutrophic and has moderate alkalinity (Figure 1b). Storefjorden has not experienced any major cyanobacterial bloom, whereas Vanemfjorden has developed massive cyanobacterial blooms due to high nutrient loading from agricultural areas in its catchment (Skarbøvik et al., 2021). These toxic cyanobacterial blooms caused a ban on bathing for several years before 2009. During the past 25 years Vanemfjorden has changed from oligohumic (<30 mg Pt L⁻¹) to mesohumic (30–90 mg Pt L⁻¹) conditions. We therefore chose to use the dataset from the Vanemfjorden basin to examine the relationship between nutrients, browning and cyanobacterial blooms. The core dataset included TP, TN, water color (mg Pt L⁻¹), chlorophyll *a* and cyanobacteria biovolume. It was downloaded from a database at the Norwegian Institute of Water Research (NIVA) and are available in Lyche Solheim and Haande (2023). The cyanobacteria data used in our analysis are the maximum biovolumes per year based on monthly samples taken between June and September. All phytoplankton analyses were performed using standardized methods (Section S1.3).

2.4 | Large-scale lake survey data

Data on phytoplankton total biovolume, cyanobacteria biovolume and proportion, TP and TN concentrations, alkalinity and

water color (cDOM) were extracted for a total of 588 lakes (Moe et al., 2023) from a large dataset (2063 lakes) originally compiled by national and regional agencies in Europe to develop ecological status assessment systems as required by the EU Water Framework Directive (WFD) (Moe et al., 2008, 2013). The selected lakes cover the whole gradient from ultraoligotrophic to hypereutrophic conditions (TP annual mean concentrations ranging from 1 to $200\,\mu g\,L^{-1}$) and the whole humic gradient from oligohumic to polyhumic conditions (color ranging from 1 to $555\,mg\,Pt\,L^{-1}$). All the selected lakes are located in Norway, Sweden, Finland, or the UK (Figure 1c), which are countries that have intercalibrated their phytoplankton assessment methods, thereby ensuring data comparability (Lyche Solheim et al., 2014). Epilimnion samples of phytoplankton, nutrients, cDOM, and other physico-chemical variables from each lake were taken at two or more occasions between July and September in at least 1 year between 1985 and 2009. Analyses are based on mean summer values for each lake, except for cyanobacteria where annual maximum values were used.

2.5 | Statistical analyses

The responses of phytoplankton to the experimental nutrient enrichment and browning were tested by Generalized Additive Mixed Models (GAMM; Wood, 2010) based on the mgcv package in R version 3.5.2 (R Core Team, 2018), which enables capturing curvilinear responses to nutrients (Carvalho et al., 2013; Zuur et al., 2009). The main environmental predictors were the measured concentrations of TP, TN, and color, as well as elapsed time from the start of each of the two experiments (Day).

Response variables were chlorophyll *a* (chl *a*), total phytoplankton biovolume (BV_{PP}), and the biovolume and percentage of the three dominant taxonomic groups of phytoplankton: cyanobacteria (BV_{CYANO} and $\%_{CYANO}$), cryptophytes (BV_{CRYPTO} and $\%_{CRYPTO}$), and chlorophytes (BV_{CHLORO} and $\%_{CHLORO}$; Figure 4). Diatoms and other phytoplankton classes with low biovolumes and proportion in most enclosures (means ≤1%) were not used as separate response variables (Figure 4). For Experiment II, the effect of deep mixing was tested by adding this environmental factor to the selected predictor variables for all response variables. The potential effect of deep-mixing on cyanotoxin concentrations was assessed by comparing pairs of deep-mixed and shallow-mixed enclosures having the same nutrient enrichment, using Tukey's honestly significant difference test. This was done for each of the three browning levels.

The GAMM analyses included data from the second until the seventh week of Experiment I and from the third day after each weekly treatment in Experiment II to allow enough time for biological responses to develop. Eight candidate models were tested (Section S6, Table S5). The Akaike Information Criterion corrected for small sample sizes (AICc; Burnham et al., 2011) was used to select the most parsimonious among the candidate models. The modelled biological responses were visualized by vis.gam

contour-plots of TP and color to depict the interaction of the two variables. They were based on the most parsimonious models where the TP × color interaction was significant ($p < .05$), or else on the best model including at least one of these two variables that was statistically significant.

The cyanobacteria biovolume data from Experiment I, from Vanemfjorden and the survey dataset from 588 northern lakes were also analysed using GAMMs to explore the consistency of the cyanobacterial response across the experimental and empirical long-term and broad-scale datasets. For this cross-dataset analysis, the two predictor variables used were TP and color, including their potential interaction (tensor). For further details, see Section S6.

3 | RESULTS

3.1 | Enclosure experiments

3.1.1 | Physico-chemical variables in Experiment I

The targeted browning and phosphorus gradients were well established at the beginning of Experiment I (Table 1a). Browning (color) greatly increased in the enclosures receiving HF, thus attenuating light and reducing Secchi depth compared to the clear controls (Figure 2). The measured TP-concentrations were largely determined by the experimental P-additions with no major influence of browning. TP ranged from 18 to $44\,\mu g\,L^{-1}$ in the clear enclosures (A1-7), from 18 to $55\,\mu g\,L^{-1}$ in the moderately colored enclosures (B1-7) and from 18 to $44\,\mu g\,L^{-1}$ in the highly colored enclosures (C1-7). After the initial increase, both color and TP declined strongly over the course of Experiment I, with TP reaching approximately the concentrations observed before the experimental additions (Figure 2). The fastest TP-decline was found in the clear enclosures. Similarly, after the initial increase, the SRP concentration was low or decreased to the detection limit in the clear enclosures. In the brown enclosures, however, the decrease of SRP was less pronounced and even increased during the first weeks after nutrient and HF-additions. The TN:TP mass ratio of 32 ± 6 in the enclosures varied little during the course of Experiment I (data not shown). HF-addition only slightly increased dissolved organic carbon (DOC) above the initial concentration of 4.5–$5.5\,mg\,L^{-1}$, reaching 5.5–6.0 and 6.0–$6.5\,mg\,L^{-1}$ in the moderately and highly colored enclosures, respectively.

Attenuation of PAR and the spectral distribution of light in the enclosures changed substantially with increased browning (Figure 3a; Section S3, Table S4). The blue and green spectral ranges were strongly attenuated by browning, the red spectral range much less. The initial ratio of euphotic depth (z_{eu}) to mixing depth (z_{mix}) was above 1 in all enclosures (Figure 3b). The ratio z_{eu}:z_{mix} remained above 1 in almost all clear enclosures during Experiment I, but dropped below 1 in enclosures receiving HF, especially when high amounts were added. The ratio increased during the course of Experiment I (Figure 3b).
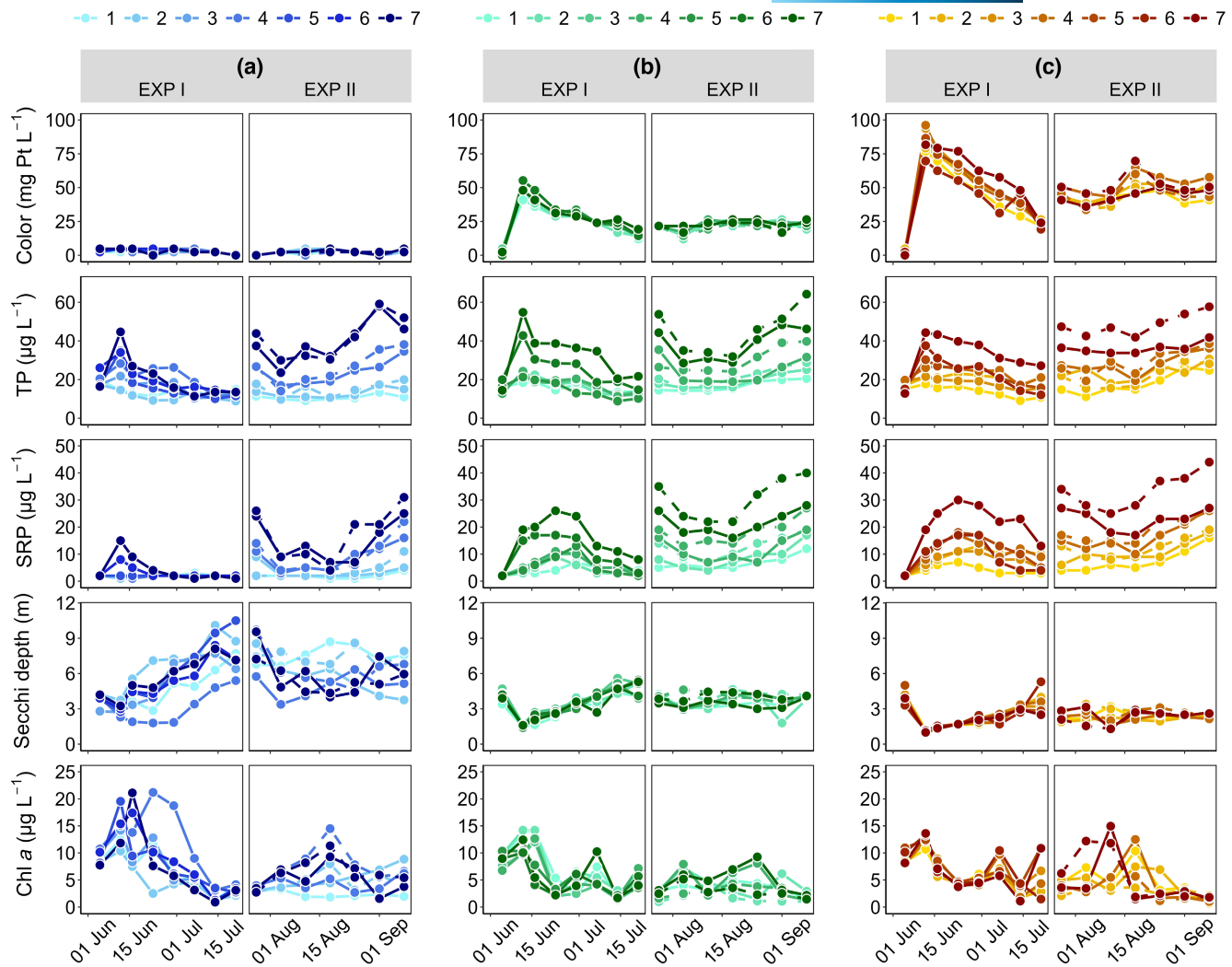
FIGURE 2 Dynamics of color, total phosphorus (TP), soluble reactive phosphorus (SRP), Secchi depth and chlorophyll *a* (chl *a*) in the 21 experimental enclosures during Experiments I and II. Three levels of experimental browning (Table 1) are illustrated by blue (A enclosures, no browning), green (B enclosures, moderate browning) and orange (C enclosures, high browning) circles and lines. Increasing concentrations along the TP gradient are indicated by color changes from light to dark (1–7, see legend on top of graphs). Deep-mixed enclosures in Experiment II is depicted by dashed lines.

3.1.2 | Physico-chemical variables in Experiment II

The weekly additions of HF were successful in maintaining the intended browning levels throughout Experiment II, as reflected by color and Secchi depth (Table 1b, Figure 2). The first nutrient addition at the beginning of Experiment II also established the intended gradient of TP concentrations (Table 1b, Figure 2). The subsequent weekly additions of P and N resulted in relatively constant TP and SRP concentrations in the low-nutrient enclosures, but showed fluctuations in enclosures with higher nutrient levels (Figure 2). However, the relative differences between nutrient levels were preserved throughout Experiment II. Deep mixing led to higher nutrient concentrations in the enclosures with medium and high browning levels and at the two highest nutrient enrichment levels, but this was not seen in the clear enclosures (Figure 2). The ratio of $z_{eu}:z_{mix}$ remained above

1 in the clear, shallow-mixed enclosures. In contrast, both deep mixing and browning resulted in ratios below 1 (Figure 3b).

3.1.3 | Phytoplankton responses in Experiment I

The initial phytoplankton community was dominated by filamentous cyanobacteria with *Dolichospermum zinserlingii* (biomass $1.0 \pm 0.4 \, mm^3 \, L^{-1}$) contributing 70% to the total phytoplankton biomass (Section S2, Figure S1, Table S3). The epilimnetic chlorophyll *a* concentration and the total phytoplankton biovolume increased immediately after the nutrient and HF additions and subsequently declined in all enclosures to concentrations lower than before the start of the experiment (Figures 2 and 4). The highest chlorophyll *a* concentrations and total biovolumes were observed in the most nutrient-enriched, clear enclosures. Significantly lower chlorophyll *a*
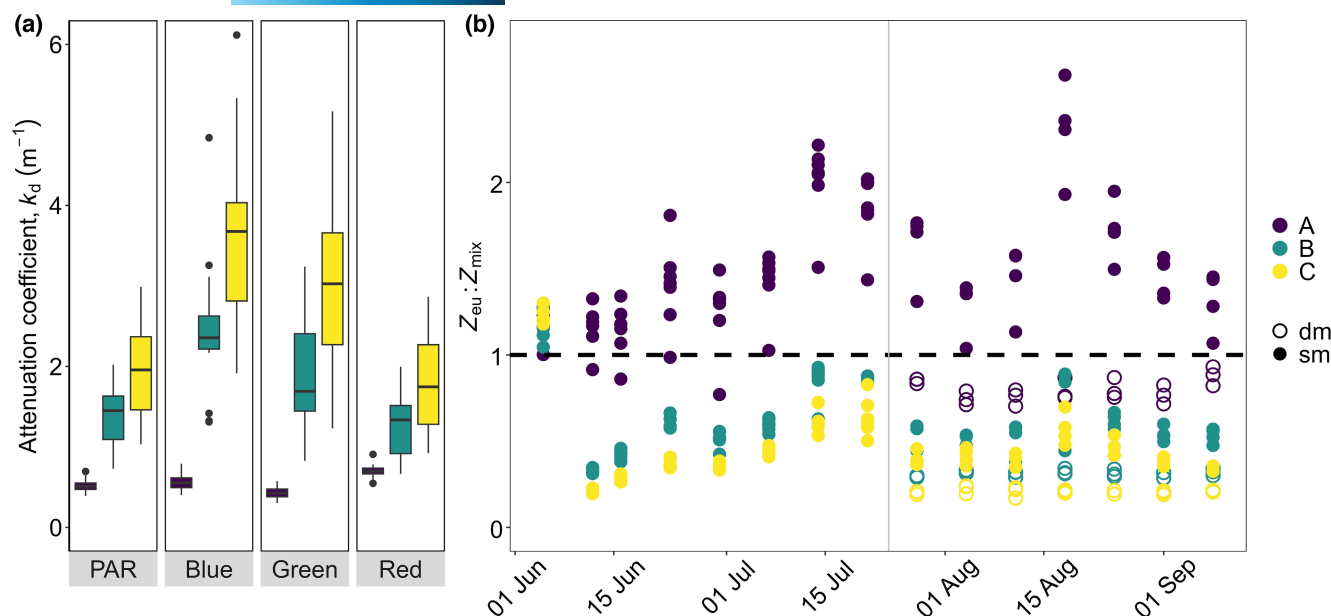
FIGURE 3 Light conditions in enclosures during Experiments I and II. (a) Light attenuation coefficient (spectroradiometer-based k_d) for four spectral ranges (PAR: 400–700 nm, blue: 430–500 nm, green: 520–565 nm, and red: 625–700 nm) in the clear (dark blue, A), moderate browning (green, B), and high browning (yellow, C) enclosures (Table 1a). All effects of browning were significant within each of the four spectral ranges ($p < .05$; Table S3). (b) Changes in the ratio between euphotic depth (z_{eu}) and mixing depth (z_{mix}) as an indicator of epilimnetic light conditions in A (clear), B (moderate browning) and C (high browning) enclosures. Thin vertical grey line in the middle indicates the transition from Experiment I to II. In Experiment II. Open circles indicate deep-mixing (dm) and filled circles shallow-mixing (sm).

concentrations and total biovolumes developed in the brown enclosures (Figures 2 and 4, Table 2).

After an initial increase in some enclosures, the cyanobacteria populations declined in all enclosures. The decline happened after 10 days in the brown enclosures, but only after 20 days in the clear enclosures (Figure 4). After the collapse of the cyanobacteria, chlorophytes and cryptophytes became the dominant phytoplankton groups. Enclosure A4 deviated from this trend in that a second peak of the cyanobacterium *Pseudanabaena limnetica* developed at the end of June, causing the highest chlorophyll *a* concentration (21 µg L⁻¹) measured during Experiment I (Figure 2). While cyanobacteria clearly responded negatively to browning and positively to nutrient enrichment, cryptophytes responded positively to browning and negatively to nutrient enrichment. Chlorophytes developed higher biovolumes in the clear than in the brown enclosures (Table 2, Figure 4). Individual chlorophyte taxa, such as *Ankyra judayi*, responded positively to nutrient enrichment in the enclosures subjected to moderate browning.

3.1.4 | Phytoplankton responses in Experiment II

The epilimnetic chlorophyll *a* concentration and total phytoplankton biovolume during Experiment II showed moderate fluctuations in response to different treatments and at different times (Figures 2 and 4). Elevated concentrations of chlorophyll *a* and total phytoplankton biovolume were observed in the middle of Experiment II in most of the nutrient-enriched enclosures

(Figures 2 and 4, Table 2). Deep mixing did not have significant effects on chlorophyll *a* concentration nor on total phytoplankton biovolume (Table 2).

The biovolume and proportion of cyanobacteria were much lower in Experiment II than in Experiment I, but the response to nutrient enrichment and browning was similar in both experiments, increasing with nutrient enrichment and decreasing with browning (Figures 4 and 5, Table 2). Cryptophytes dominated in enclosures when browning levels where moderate or high. Chlorophytes responded negatively to browning and positively to nutrient enrichment. Different species of chlorophytes and *conjugatophytes* became dominant in the clear enclosures, in those that were most enriched with nutrients. Specifically, *Chlamydomonas* sp. was dominant or co-dominant in enclosures A5, A6 and A7, *Closterium aciculare* in enclosure A6, and *Monomastix* sp. in enclosures A6 and A7. *Chlamydomonas* sp. was also quite dominant in the most nutrient-enriched enclosures at the medium browning level. Including deep mixing as an additional predictor variable did not significantly improve the model prediction for most of the response variables, except for cryptophyte biovolume, which significantly decreased (BV_CRYPTO, $p = .03$) (Table 2).

3.1.5 | Grazing pressure

Mesozooplankton biomass was much higher in the clear than in the brown enclosures in both experiments (Figures S4 and S5). However, the zooplankton:phytoplankton carbon ratio (Z:P in Figure 4), used
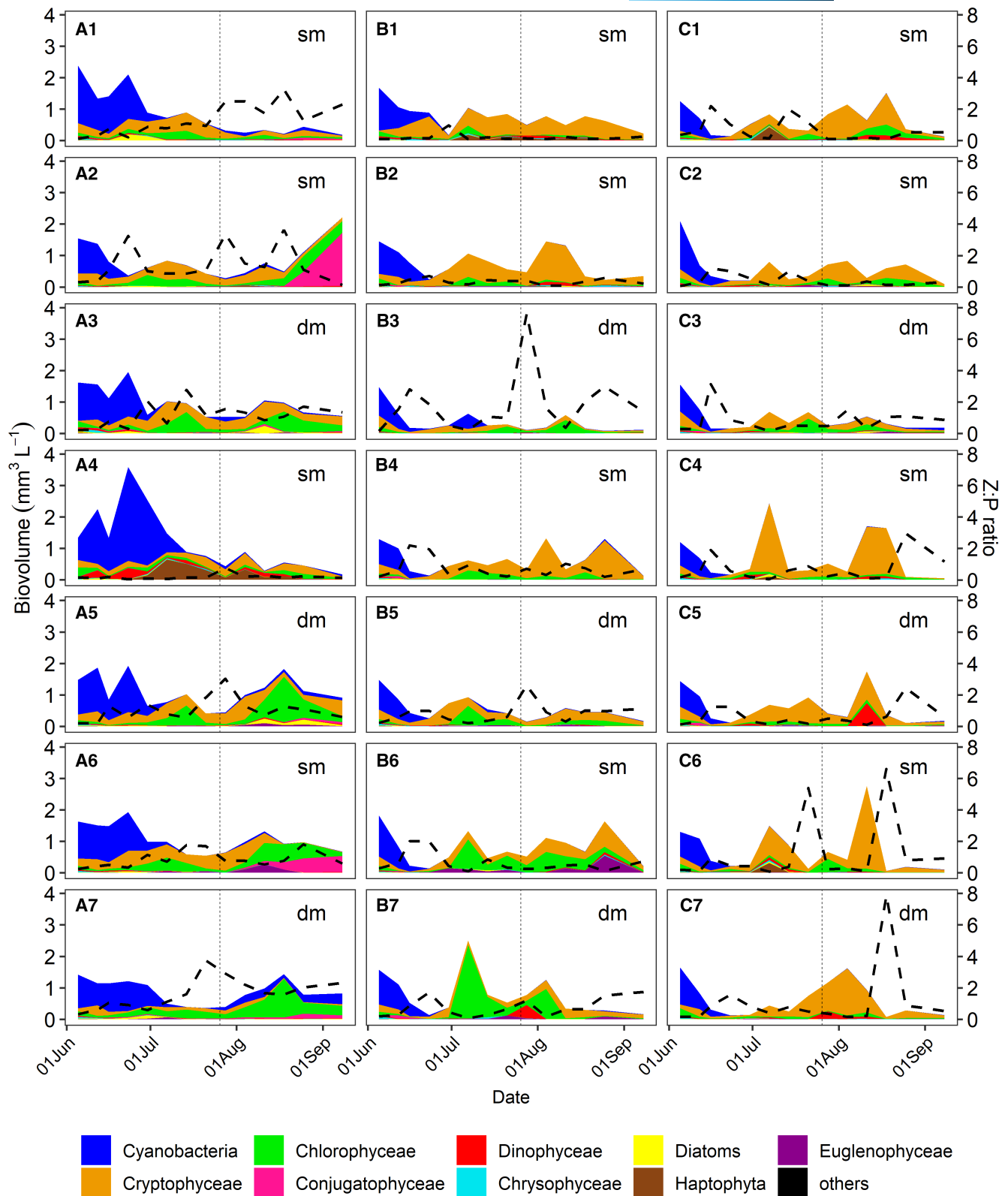
FIGURE 4 Phytoplankton community response (see taxonomic classes in legend) and the zooplankton:phytoplankton carbon ratio (Z:P, dashed lines) as a proxy for grazing pressure in the 21 enclosures. Experiments I and II are separated by vertical light grey lines. Nutrient supply successively increased along the gradient from enclosure 1 to 7 in Experiment I, and were coupled in shallow- and deep-mixed pairs of increasing nutrients in Experiment II (Table 1). Browning treatments were A=clear enclosures with no HF added, B=medium and C=high levels of HF.

TABLE 2 Results of the most parsimonious GAMM models (E, F, G, H) among eight candidate models tested (Table S5) for both Experiments I and II. Predictor variables were color, total phosphorus (TP), total nitrogen (TN), elapsed time (Day) and, in Experiments II, mixing regime. The selected models show a significant interaction between color and TP concentration for most of the response variables. The F-values are a test statistic of the GAMM analysis, p denotes the significance level of the predictors, R^2 is the variability in the response variable explained by the model. Response variables were chlorophyll a (chl a), total phytoplankton biovolume (BV_{TOTAL}), biovolume of cyanobacteria (BV_{CYANO}), cryptophytes (BV_{CRYPTO}) and chlorophytes (BV_{CHLORO}), as well as the biovolumes of these three major taxonomic classes relative to the total phytoplankton biovolume (%BV). The p-values in bold font indicate the significant predictor variables.

Experiment I response variable	Model	Predictor variable	F	p	R²
Chl a	H	Color, TP	11.0	**<.0001**	.43
		Day	3.0	.09	
		TN	1.6	.21	
BV_{TOTAL}	G	Color, TP	9.1	**<.0001**	.42
		TN	3.8	.08	
BV_{CYANO}	F	Color, TP	17.0	**<.0001**	.70
		Day	11.5	**<.0001**	
%BV_{CYANO}	H	Color, TP	21.8	**<.0001**	.66
		Day	42.4	**<.0001**	
		TN	1.8	.19	
BV_{CRYPTO}	E	Color, TP	0.9	.40	.02
%BV_{CRYPTO}	E	Color, TP	5.1	**<.0001**	.29
BV_{CHLORO}	F	Color, TP	6.6	**<.0001**	.54
		Day	4.5	**.003**	
%BV_{CHLORO}	H	Color, TP	3.5	**.02**	.20
		Day	7.8	**.001**	
		TN	2.4	.18	
Experiment II response variable	**Model**	**Predictor variable**	**F**	**p**	**R²**
Chl a	F	Color, TP	2.2	**.03**	.26
		Day	7.5	**.001**	
		Deep-mixing	−0.5	.63	
BV_{TOTAL}	F	Color, TP	2.5	.09	.14
		Day	11.0	**<.001**	
		Deep-mixing	−1.3	.22	
BV_{CYANO}	E	Color, TP	3.4	**.04**	.23
		Deep-mixing	1.3	.21	
%BV_{CYANO}	E	Color, TP	1.9	.10	.16
		Deep-mixing	1.1	.28	
BV_{CRYPTO}	F	Color, TP	2.1	.10	.18
		Day	17.8	**<.0001**	
		Deep-mixing	−2.2	**.03**	
%BV_{CRYPTO}	F	Color, TP	5.2	**.0001**	.42
		Day	5.0	.05	
		Deep-mixing	−0.9	.37	
BV_{CHLORO}	F	Color, TP	4.2	**<.0001**	.32
		Day	3.5	**.02**	
		Deep-mixing	1.2	.25	
%BV_{CHLORO}	F	Color, TP	2.3	.06	.19
		Day	3.4	**.03**	
		Deep-mixing	1.8	.07	
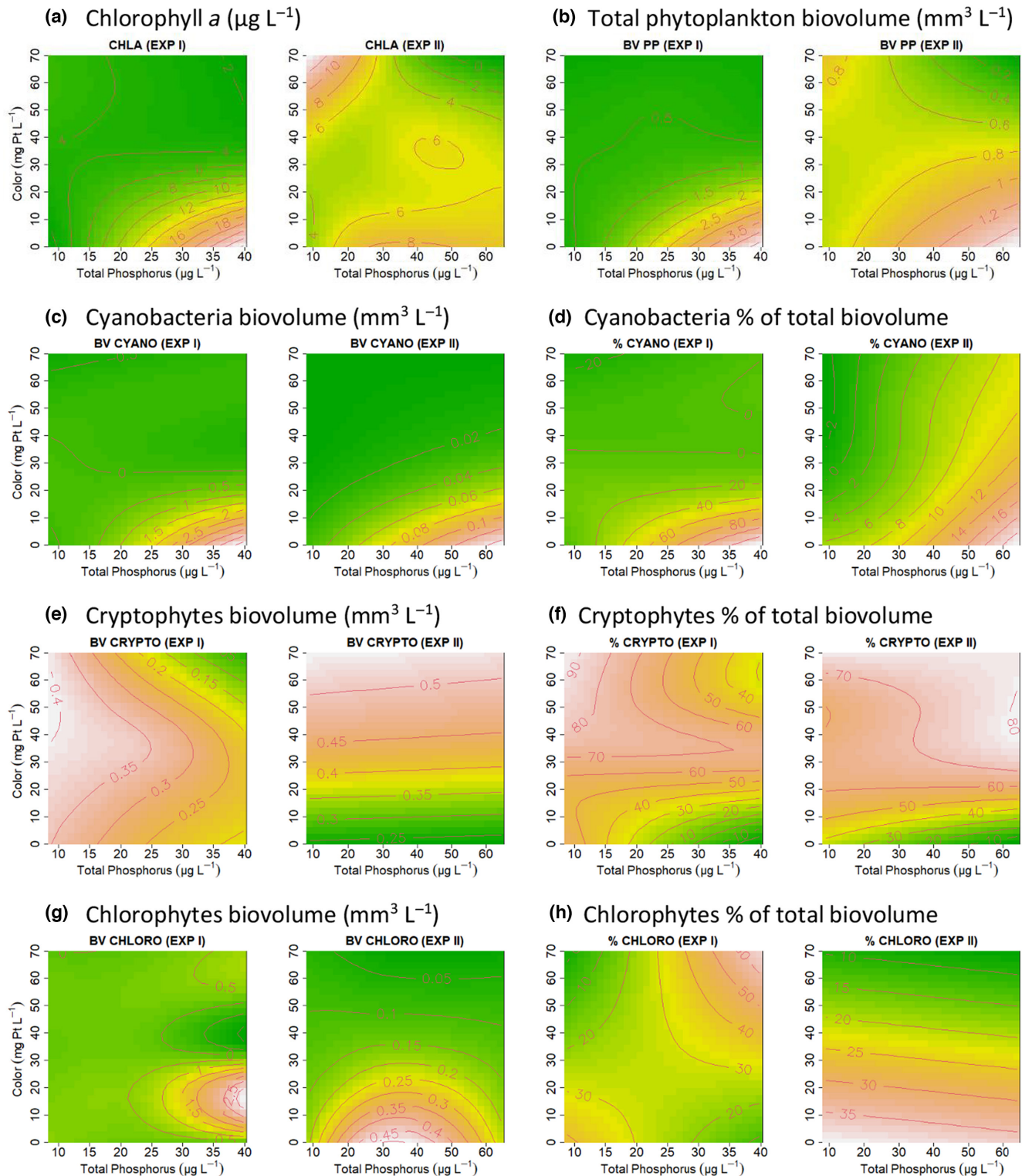
FIGURE 5 Contour plots of the modelled interaction effect of total phosphorus and browning (color) on phytoplankton in Experiments I and II. The contours (numbers given on the contours) range from low (green) to high (red) values. Selected models show significant interactions between total phosphorus and color for all response variables except BV_{TOTAL} (Experiment II), %BV_{CYANO} (EXP II), BV_{CRYPTO} (Experiments I and II) and %BV_{CHLORO} (Experiment II). For details on the models, see Table 2.

as a proxy for grazing pressure, did not show clear differences among enclosures in Experiment I. In the clear enclosures, mesozooplankton biomass was positively affected by nutrient additions at the end of Experiment I (Figure S4). The only exception was enclosure A4, which

was dominated by a large predatory calanoid copepod (*Heterocope appendiculata*).

In Experiment II, the Z:P ratio was slightly higher in the clear than in the brown enclosures at the two lowest nutrient levels. The

mesozooplankton biomass was much higher in the clear than in the brown enclosures (Figures S4 and S5). The Z:P maxima occurred between peaks of cryptophyte biovolumes (Figure 4) in two of the brown enclosures (C6 and C7) indicating potentially heavy grazing on cryptophytes. The Z:P ratio and mesozooplankton biomass tended to be higher in the deep-mixed enclosures than in shallow-mixed enclosures at similar nutrient concentrations (Figure 4, Figures S4 and S5).

3.1.6 | Combined effects on phytoplankton responses across experiments

The most parsimonious GAMM models (Table 2) analysed separately for the two experiments revealed that browning counteracted the effect of nutrient enrichment on cyanobacterial biovolume (BV_{CYANO}) and the proportion of total biovolume (%BV_{CYANO}) in both experiments (Figure 5; Table S5). Elapsed time and TN were contributing co-variables, with time being more important than TN (Table 2). The model explaining most of the variation in the data (R^2) was for total cyanobacterial biovolume in Experiment I (BV_{CYANO}, $R^2 = .70$) followed by the proportion of cyanobacteria of the total biovolume (%BV_{CYANO}, $R^2 = .66$). Cryptophyte biovolume and proportion of the total phytoplankton biovolume showed no clear responses along the nutrient gradient but a positive response to browning, while chlorophytes clearly responded negatively to browning (Figure 5).

3.1.7 | Cyanotoxins

Microcystin was detected in quantifiable amounts, while saxitoxin, cylindrospermopsin, and anatoxin were below their detection limits. The microcystin concentration during Experiment I was high only in the clear enclosures with nutrient additions above $20\,\mu g\,TP\,L^{-1}$. The maximum concentration was $6.9\,\mu g\,L^{-1}$ (Figure 6). Microcystin concentration was very weakly related with the total biovolume of all cyanobacteria across both experiments ($R^2 = .08$; Figure S3). However, the relationship was much stronger with the biovolume of *Planktothrix rubescens* ($R^2 = .62$; Figure S3), reaching $0.3–1.2\,mm^3\,L^{-1}$ at the end of June in the clear enclosures receiving high levels of nutrients (A5, A6, A7). The microcystin concentrations were low in all enclosures subjected to browning in Experiment I ($<0.3\,\mu g\,L^{-1}$), consistent with the low biovolume of *Planktothrix rubescens* in those enclosures ($<0.2\,mm^3\,L^{-1}$).

The microcystin concentration measured during Experiment II was much lower than during Experiment I (Figure 6) but showed a significant positive response to deep mixing in the clear enclosures at the two highest levels of nutrient addition (Figure S2). The average biovolume of *Planktothrix rubescens* was an order of magnitude higher in the deep-mixed ($0.1\,mg\,L^{-1}$) than in the shallow-mixed clear enclosures ($0.01\,mg\,L^{-1}$). The concentration in all enclosures subjected to browning in Experiment II was very low ($<0.04\,\mu g\,L^{-1}$), similar to the results of Experiment I (Figure 6).

## 3.2 | Development of cyanobacteria in a long time series from Lake Vansjø, Norway

The TP concentration in Vanemfjorden was around $30\,\mu g\,L^{-1}$ in 1996, increasing to $35–40\,\mu g\,L^{-1}$ during 2001–2006. The subsequent gradual decline towards the WFD good/moderate boundary value of $20\,\mu g\,TP\,L^{-1}$ set for humic Norwegian lakes of moderate alkalinity (Figure 7a) followed the implementation of phosphorus reduction measures. The chlorophyll *a*-concentration remained high until 2009, with a peak reached in 2007, and then decreased towards the WFD good/moderate boundary value. Concentrations of humic substances in the basin fluctuated over same 25-year period with an overall increasing trend from oligohumic to mesohumic (Figure 7b). However, there were large fluctuations between 1999–2007 with a peak in 2001. This peak occurred after a major flood in late autumn 2000, while the decreasing color down to oligohumic levels in 2003–2006 happened during drier years (data on precipitation from the nearby weather station at Rygge). Cyanobacterial blooms were absent between 2000 and 2003, but temporarily reappeared between 2004 and 2007 before declining to low values (Figure 7d). The pronounced changes in maximum cyanobacterial biovolume between 2000 and 2009 did not match the development of phosphorus and chlorophyll *a* but inversely mirrored the fluctuations in water color (Figure 7). Since 2010, however, the cyanobacterial biomass has been very low, while the color has been above $35–40\,mg\,Pt\,L^{-1}$ and the TP has been below $30\,\mu g\,L^{-1}$ (Figure 7; Figure S6).

## 3.3 | Broad-scale patterns of cyanobacterial blooms in relation to browning and nutrients

The 588 lakes in Norway, Sweden, Finland and UK with $TP < 200\,\mu g\,L^{-1}$ showed differences in cyanobacteria responses to TP in clearwater (color $<40\,mg\,Pt\,L^{-1}$) versus humic lakes (color $>40\,mg\,Pt\,L^{-1}$; Figure 8). In the clearwater lakes, the maximum biovolume and proportion of cyanobacteria was higher than in humic lakes at TP concentrations $<100\,\mu g\,L^{-1}$. When TP exceeds $100\,\mu g\,L^{-1}$, the biovolume and proportion of cyanobacteria is very high and similar in both clear and humic lakes.

3.4 | Comparison of cyanobacteria responses to phosphorus and water color across the experimental and observational approaches

The main patterns of cyanobacterial biovolume in relation to TP concentrations and browning were similar across the three approaches we used (Figure 9), increasing with nutrient enrichment and decreasing with browning. The relationships are highly significant for all three data sets (Table 3), although the proportion of explained variation (R^2) decreases from 70% for the experiments (dominated by *Dolichospermum zinserlingii*) to 51% for the time series from Vanemfjorden (dominated by *Microcystis aeruginosa* before
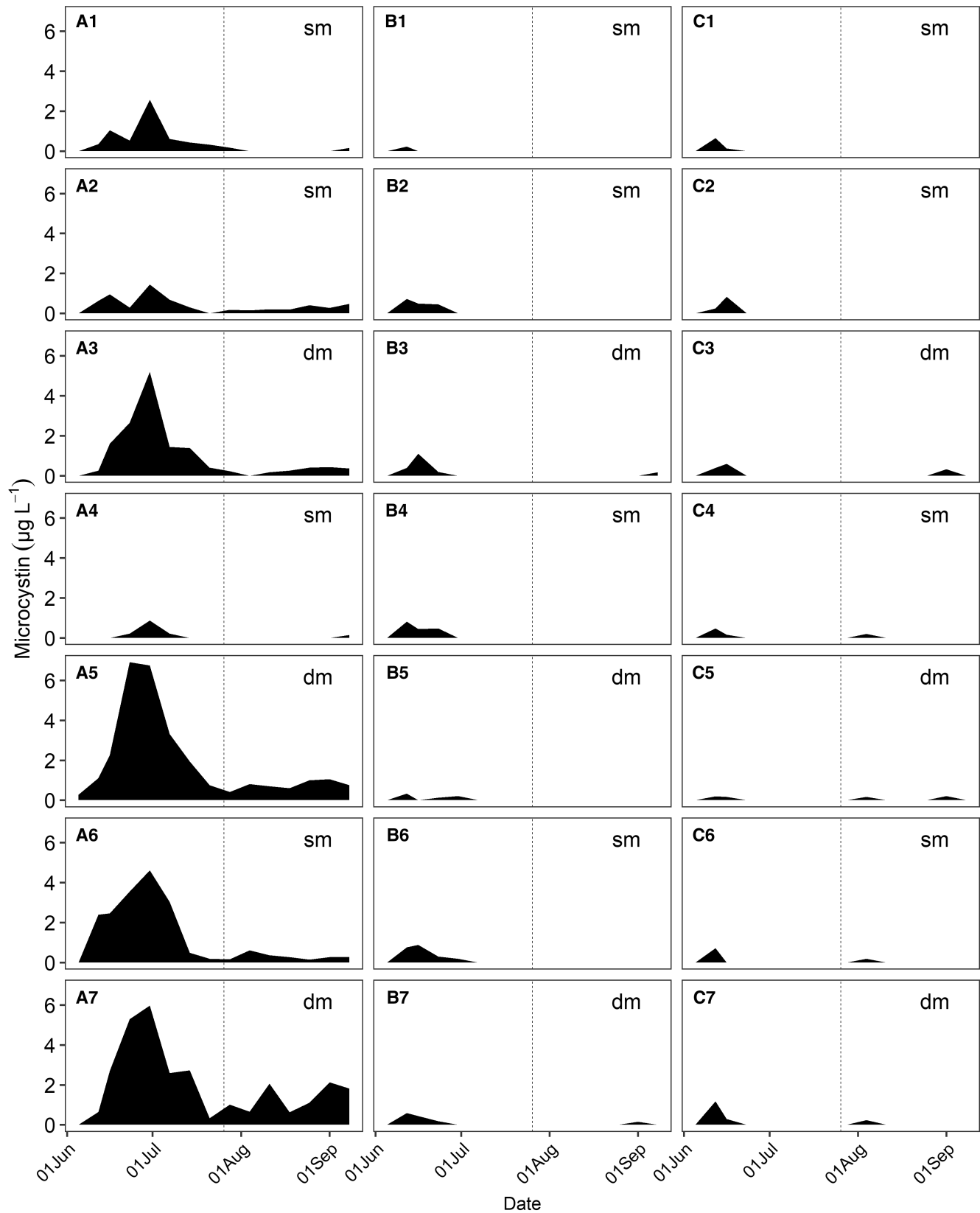
FIGURE 6 Microcystin concentrations in 21 enclosures during Experiments I and II, which are separated by vertical dotted lines. See Figure 4 for further details on labels A, B, C. The nutrient gradient increases from enclosure 1 to 7 in Experiment I and were coupled in shallow and deep mixed pairs of enclosures with increasing nutrients in Experiment II. Browing treatments were A=clear enclosures with no HF added, B=medium and C=high level of added HF (Table 1).
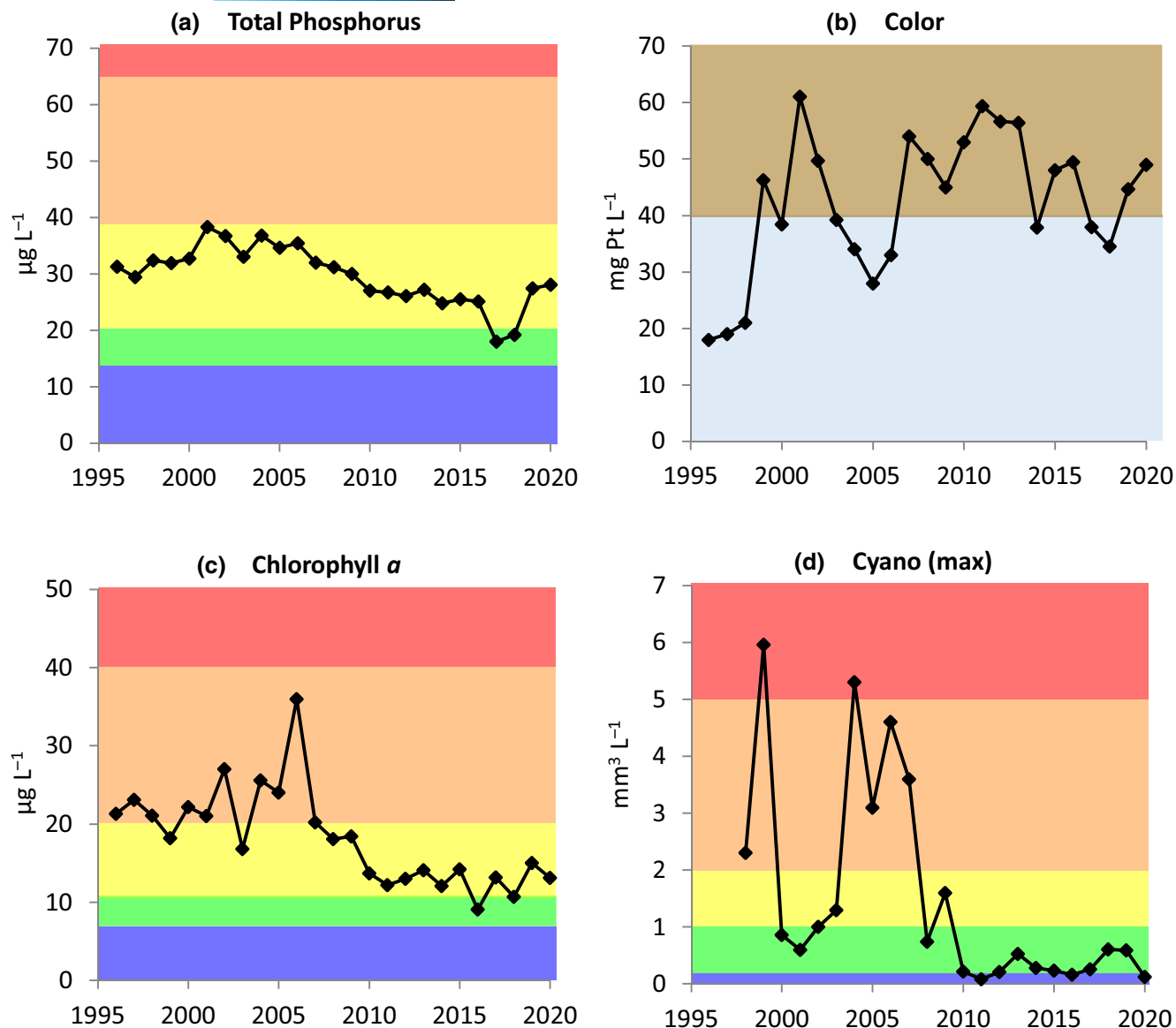
FIGURE 7 Long-term changes of summer mean values (June–September) from 1995 to 2020 in the Vanemfjorden basin of Lake Vansjø, Norway, for (a) Total Phosphorus concentration, (b) Color (browning), (c) Chlorophyll *a*, and (d) Cyano (max) (maximum biomass of cyanobacteria). The color code in panels a, c, d represents the official Norwegian type-specific ecological status classes of the WFD (blue = high, green = good, yellow = moderate, orange = poor, and red = bad). The color code in panel b indicates clear (oligohumic) level in light blue and mesohumic level in beige.

browning) and only 4% for the survey of 588 lakes representing a wide range of physico-chemical characteristics (e.g., alkalinity, mean depth, water residence time) and cyanobacteria species. Despite the fundamental differences in the nature of the three data sets, they returned not only the same general shape of the relationships, but also suggested similar TP-concentrations (10–20 μg L^{-1}) at which cyanobacteria are likely to exceed a biovolume of 1 mm^3 L^{-1} (corresponding to the WHO low risk threshold; (Section S5) in oligohumic lakes). However, in more humic lakes, the cyanobacteria exceeded the low-risk threshold only at considerably higher TP-concentrations (20–30 TP L^{-1}) (Figure 9). In Experiment I, this biovolume threshold was not exceeded when the water color was >25 mg Pt L^{-1} even at the highest TP-concentration. Cyanobacteria

had very low biovolume in the epilimnion during Experiment II, never exceeding this biovolume threshold.

4 | DISCUSSION

4.1 | Aims and main findings

In this paper, we aimed to determine the combined effects of browning and nutrient enrichment on phytoplankton communities, with particular attention to harmful cyanobacteria. We found that browning decreased the impact of nutrient enrichment on phytoplankton biovolume and shifted the species composition from autotrophic taxa
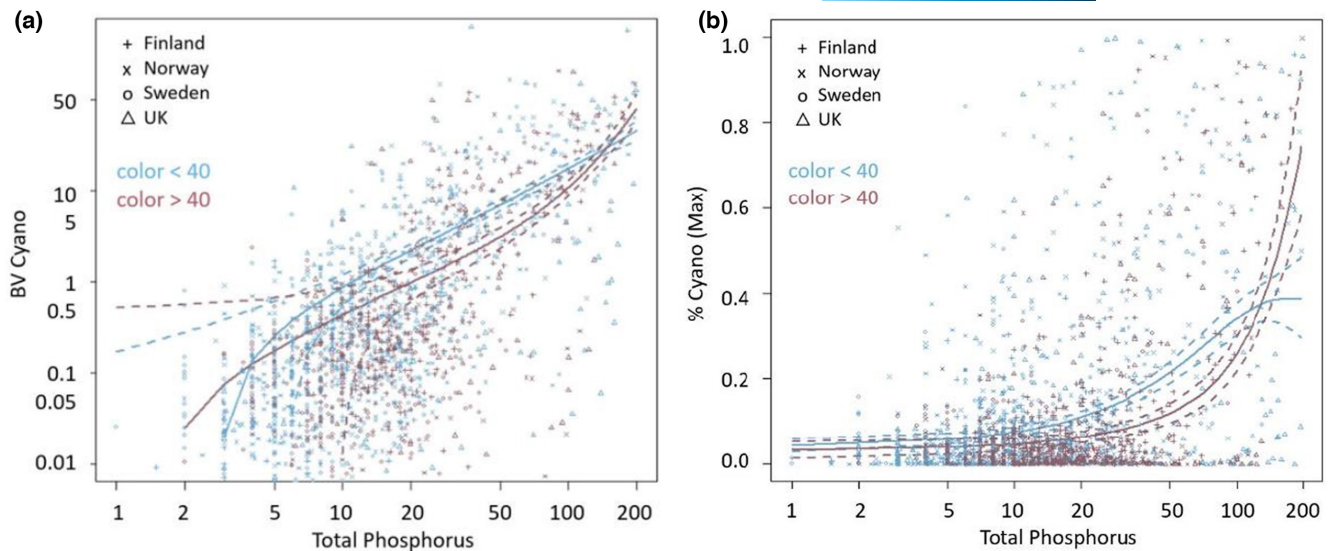
FIGURE 8 Maximum cyanobacterial biovolumes (BV_{Cyano} in $mm^3 mL^{-1}$) (a) and percentage of cyanobacteria of the total phytoplankton biovolumes (b) as a function of total phosphorus ($\mu g L^{-1}$) < 200 $\mu g L^{-1}$ during summer (June–September) in 588 lakes from Norway, Sweden, Finland and the UK divided into clearwater (oligohumic) lakes (color <40 mg Pt L^{-1}, number of lake years = 1363) and humic lakes (color >40 mg Pt L^{-1}, number of lake years = 830). Note $\log_{10}$ scale on the x-axis in both panels and on the y-axis of the left panel.
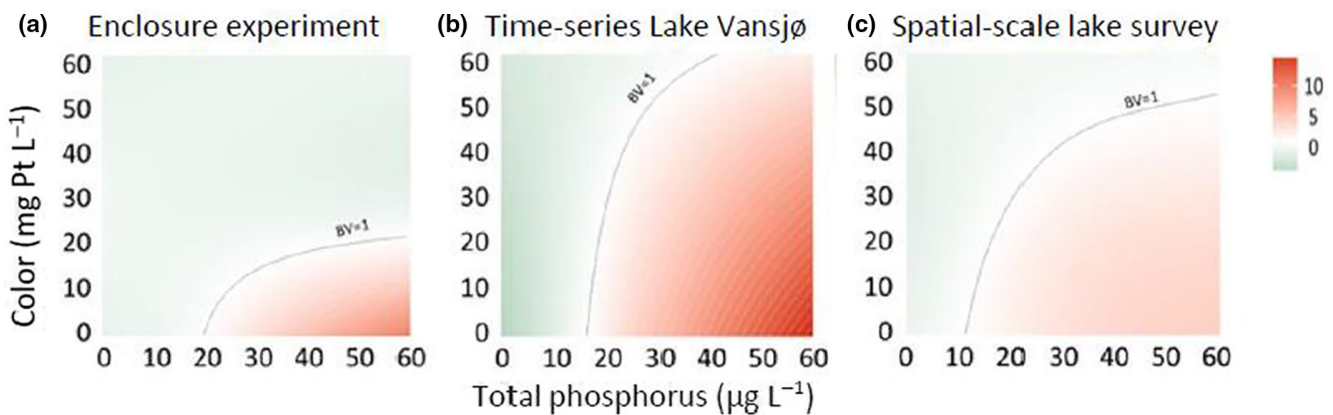
FIGURE 9 GAMM results showing biovolumes (BV) of cyanobacteria (as $mm^3 L^{-1}$) (blue-green to red colors and numbers given in legend on the right side) in relation to color and total phosphorus concentrations in three independent data sets: (a) Experiment I, all the data were used (b) lake Vansjø-Vanemfjorden, annual maximum biovolume (c) broad spatial-scale dataset. Grey lines indicate biovolumes of 1 $mm^3 L^{-1}$.

TABLE 3 Summary of results from GAMMs assessing the influence of water color and phosphorus supply on the biovolume of cyanobacteria in lakes during summer. For the Experiment I, all the data were used, while annual maximum biovolume was used in the lake Vansjø-Vanemfjorden and in the broad spatial-scale dataset.

Dataset	Predictive variable	F-value	p-value	R^2
Experiment I	Color, TP	17.0	<.0001	.70
Time-series of Lake Vansjø	Color, TP	9.1	.004	.51
Broad-scale lake survey	Color, TP	8.5	<.0001	.04

to mixotrophic flagellates. We also aimed to investigate how storm-induced deep mixing interacts with nutrient enrichment and browning to affect phytoplankton communities. We found that deep-mixing decreased the biovolume of mixotrophic cryptophytes but increased

the cyanotoxins in the nutrient-enriched clear enclosures. Finally, we aimed to provide guidance to improve nutrient management for stratifying lakes, offering TP thresholds above which cyanobacterial blooms are likely to develop in clearwater and in humic lakes.

4.2 | Importance of underwater light conditions induced by browning

Irradiance and spectral composition are critical factors affecting primary production, and hence important in governing competitive outcomes in phytoplankton communities (Dubinsky & Stambler, 2009; Huisman et al., 1999; Stomp et al., 2007). Therefore, strong changes in underwater light conditions by browning are expected not only to restrain phototrophs as a whole but also to shift phytoplankton community structure (Bergström & Karlsson, 2019). Community changes from cyanobacteria to mixotrophic species have been reported from Canadian lakes with high water color (Senar et al., 2021). Our results are in line with these expectations, and indicate light-limitation of autotrophic phytoplankton growth in response to browning (Diehl et al., 2015; Shatwell et al., 2012). Our results show, however, that the suppression of cyanobacteria by browning in stratified lakes is limited to TP concentrations $<100\,\mu g\,L^{-1}$. This is further discussed in the section on nutrient impacts below.

Despite these multiple lines of evidence, the consistent suppression of cyanobacteria exposed to browning seems counter-intuitive considering the effective vertical migration ability of cyanobacteria by means of gas vacuoles (Deacon & Walsby, 1990). Moreover, their accessory pigments (phycoerythrin and phycocyanin) enable cyanobacteria to capture light at longer wavelengths, which is less absorbed by cDOM than shorter-wavelength light (Erratt et al., 2021; Stomp et al., 2007). Although light requirements vary widely among species and strains of cyanobacteria, some taxa (e.g., *Planktothrix* and other filamentous Oscillatoriales) tolerate shade (Huisman et al., 1999; Reinl et al., 2021; Reynolds et al., 2002; Zapomělová et al., 2010), often forming a DCM below the thermocline in clearwater lakes, including Lake Stechlin (Kasprzak et al., 2017; Posch et al., 2012). These features would suggest that low light levels caused by browning are less detrimental to these cyanobacteria than to most other types of phototrophic phytoplankton. However, other cyanobacteria, including some *Dolichospermum* species, are more sensitive to dim light, which has been ascribed to high energy demands for N fixation (Reynolds et al., 2002). This may explain why the dominant cyanobacterium in our enclosure experiments, *Dolichospermum zinserlingii*, declined more quickly in the brown than in the clear enclosures. Our results indicate that *Dolichospermum* in our experiments, *Microcystis* in Vanemfjorden and chlorophytes are less competitive than mixotrophic cryptophytes under dim light, especially when nutrient concentrations are $<100\,\mu g\,TP\,L^{-1}$ (Phillips et al., 2013). This suggests mixotrophy as the most plausible species trait accounting for the success of cryptophytes in the brown enclosures (Calderini et al., 2022; Grujcic et al., 2018; Hansson et al., 2019). Increasing dominance of mixotrophic phytoplankton under conditions of browning in stratified lakes has also been repeatedly reported by others (Bergström et al., 2003; Deininger et al., 2017; Wilken et al., 2018). In humic lakes with very high nutrient concentrations

($>100\,\mu g\,TP\,L^{-1}$), some cyanobacteria might still outcompete mixotrophic flagellates because of nutrient saturation and self-shading, which is likely to limit the competitive advantage of both mixotrophs and fast-growing chlorophytes requiring bright light. This could explain the lack of significant differences between the total biovolume and proportion of cyanobacteria in clearwater versus humic lakes when TP concentrations exceed $100\,\mu g\,L^{-1}$ (Figure 8).

4.3 | Impacts of nutrient enrichment

Contrasting with the strong browning effect, the low-moderate impact of nutrient enrichment on phytoplankton community dynamics in our experiments is remarkable. Although cyanobacteria increased with nutrient enrichment in the enclosures without browning (Figure 5) in line with Carvalho et al. (2013), this enrichment was unable to counter the disappearance of the initially dominant cyanobacteria. The lack of a consistent nutrient stimulation on cyanobacteria growth in the brown enclosures can be attributed to the overwhelming impact of browning-induced light limitation, as discussed above.

However, other mechanisms must play a role to account for the decline observed in the absence of browning. One possibility is potentially high zooplankton grazing in the clear enclosures (Figure 4, Figures S4 and S5). However, given the grazing resistance of filamentous cyanobacteria, this possibility was unlikely to be of major importance (Lürling, 2021). Another possible explanation is that periphyton on the enclosures walls depleted the nutrients, causing the cyanobacteria to produce resting stages (akinetes) that sedimented, especially in the clear enclosures not affected by browning. This notion is supported by the depletion of SRP after 3 weeks in Experiment I (Figure 2). However, the proportion of nutrients captured by periphyton was estimated to be less than 15% of the nutrient pool in the epilimnion (Table S6) in both the clear and humic enclosures, which makes this explanation unlikely as well. Alternatively, cyanophages or chytrids, which infect cyanobacteria in Lake Stechlin (Van den Wyngaert et al., 2022), could have played a role, but we do not have specific data from our experiment to substantiate this disease hypothesis. Thus, the most parsimonious explanation for the cyanobacteria decline is a natural phenological shift in the plankton community (Sommer et al., 2012), as also observed in the epilimnion of the lake during Experiment I (data not shown).

The only expected trend relating to nutrient enrichment was the promotion of chlorophytes, although intense browning prevented even this response. Due to high potential grazing pressure by zooplankton (Z:P > 0.5), this stimulation may have been lower in our experiments than in lakes with zooplanktivorous fish, where Z:P is normally <0.5 (Jeppesen et al., 2011). Nevertheless, the stimulation of chlorophytes in conditions of less severe light limitation is in accordance with the resource-acquisition traits of these taxa and high maximum growth rates (e.g., Schwaderer et al., 2011).

4.4 | Effects of deep mixing on phytoplankton biovolume and composition

High turbulence in deeply mixed water columns prevents effective buoyancy regulation by gas vacuoles, implying an adverse influence of mixing on cyanobacteria in turbulent conditions (e.g., Huisman et al., 1999; Posch et al., 2012). Our long-term data from Vanemfjorden support this conclusion, as high biovolumes of cyanobacteria were restricted to calm periods (Moe et al., 2019). Consequently, deep mixing has been proposed as an engineering measure to suppress cyanobacterial blooms (Visser et al., 2016). The results of our enclosure experiments, in contrast, show only weak effects of deep mixing on cyanobacteria and most other taxa of the phytoplankton community. Cryptophytes were the only group that showed a significant negative response to deep-mixing. One reason could be that flagellates are generally favored in shallow epilimnia or stable stratification (Huisman et al., 1999; Reynolds, 1984), and are disfavored when exposed to high turbulence or fluctuating light conditions accompanying turbulence (Guislain & Köhler, 2022; Köhler et al., 2018).

In contrast, deep mixing events can disrupt the thermal summer stratification of deep lakes, thereby redistributing nutrients and metalimnetic cyanobacteria into the epilimnion where light is available, thus providing excellent growth conditions (Giling et al., 2017; Stockwell et al., 2020). The biovolume of *Planktothrix rubescens*, a species often forming a DCM in Lake Stechlin (Padisák et al., 2010; Selmeczy et al., 2016), was 10 times higher in the most nutrient-enriched deep-mixed enclosure than in the corresponding shallow-mixed enclosure ($0.1\,\text{mm}^3\,\text{L}^{-1}$ vs. $0.01\,\text{mm}^3\,\text{L}^{-1}$). The large difference was most likely related to upwelling of a metalimnetic population of *P. rubescens*, as indicated by the red coloration of seston retained on membrane filters from all deeply mixed epilimnia and the significantly higher cyanotoxin concentrations in these enclosures. Taken together, these patterns and relationships indicate that storm-induced deep-mixing in stratified lakes can promote cyanobacterial blooms if a metalimnetic layer of cyanobacteria is present (Giling et al., 2017; Kasprzak et al., 2017) but also limit them in the absence of such a layer (Gastineau & Soden, 2009; Moe et al., 2019). The specific responses depend on the prevailing nutrient and light conditions (Berger et al., 2010; Diehl et al., 2015) and hence on browning (Bergström & Karlsson, 2019).

4.5 | Cyanotoxin responses to nutrient enrichment, browning and deep mixing

Cyanotoxin concentrations essentially followed the patterns of cyanobacterial biovolumes, although the cyanotoxin peaks lagged slightly behind the development of cyanobacteria biovolumes in most enclosures, suggesting that the toxins were primarily produced towards and after cyanobacteria reached peak abundances, when nutrient limitation or parasite infection were most likely (Chorus & Welker, 2021; Huisman et al., 2018). Two additional observations

are particularly worth noting: First, high concentrations of up to $6.9\,\mu\text{g}\,\text{microcystin}\,\text{L}^{-1}$, which clearly exceeded the WHO low-risk threshold of $1\,\mu\text{g}\,\text{L}^{-1}$ for safe drinking water consumption (Chorus & Welker, 2021), were restricted to clear enclosures with $>20\,\mu\text{g}\,\text{TP}\,\text{L}^{-1}$ identified as the critical levels for cyanobacterial development (Carvalho et al., 2013). A possible reason for the association of browning with low cyanotoxin concentrations is that toxin production is energy costly. This would suggest that light limitation caused by browning altered the resource allocation of cyanobacteria compared to the situation in clear lakes (Kardinaal et al., 2007). It is also possible that microcystin produced in those conditions was adsorbed to humic substances, leading to an underestimation of toxin production by our ELISA analyses (De la Cruz et al., 2012). However, such matrix effects were unlikely to be important, because the concentrations of humic substances in our experiments were well below the threshold of $10\,\text{mg}\,\text{L}^{-1}$ at which the ELISA test kit manufacturer identified potential for assay interference.

A second important point is that although the dominant cyanobacterium in Experiment I, *Dolichospermum*, can produce microcystin (Dreher et al., 2019), total cyanobacterial biovolume was only weakly correlated with microcystin concentration (Figure S3). Instead, cyanotoxin concentrations showed a clear positive relationship with the biovolume of *Planktothrix rubescens* (Figure S3). These relationships match previous field data from Lake Stechlin where microcystin concentrations of $27\,\mu\text{g}\,\text{L}^{-1}$ could not be attributed to the dominant species, *Dolichospermum circinalis*, but were correlated with the appearance of less abundant taxa such as *Planktothrix rubescens* (Dadheech et al., 2014). Together, these experimental and field studies thus underline the importance of considering species-level—and potentially strain-level (e.g., Hellweger et al., 2022)—relationships between cyanobacteria and cyanotoxin production when attempting to forecast risks to water quality arising from interactive effects of nutrient and cDOM supply and storm-induced deep mixing of stratified clearwater lakes.

4.6 | Interactions of multiple stressors

Evidence from both our experimental and observational results demonstrate that browning and nutrient enrichment have opposing effects on autotrophic phytoplankton (see also Birk et al., 2020; Côté et al., 2016; Spears et al., 2021). Specifically, browning counteracted the nutrient stimulation of phytoplankton by nutrient enrichment, most likely by blocking incident light. This not only limited phytoplankton growth but also shifted the species composition from cyanobacteria to mixotrophic cryptophytes, which developed in brown waters—unless they were restrained by deep mixing. In fact, when a DCM forms in clear stratified lakes, deep-mixing can amplify the stimulation of phytoplankton by nutrient enrichment, because cyanobacterial biomass is mixed into the epilimnion where light and nutrient limitation is alleviated (Giling et al., 2017, Kasprzak et al., 2017). In the absence of a DCM, however, deep mixing would counteract the stimulatory effect of nutrients because both

turbulence and the lowered average light availability resulting from a deepend epilmnion hamper phototrophic phytoplankton (Moe et al., 2019), including cyanobacteria and mixotrophic flagellates. Similarly, deep mixing is likely to exacerbate the adverse effects of browning on phytoplankton by aggravating light limitation (Berger et al., 2006; Diehl et al., 2015).

4.7 | Lake management implications

Understanding the complex interplay of multiple stressors and the combined impacts on phytoplankton communities, including risks of harmful algal blooms, is important to adapt current lake management strategies (Carvalho et al., 2013; Côté et al., 2016; Poikane et al., 2019). An important message for lake management from our results is, therefore, that browning effectively suppresses cyanobacterial blooms in stratifying lakes up to a high TP concentration of $100\,\mu g\,L^{-1}$ (Figure 8). Above this TP concentration, the effects on phytoplankton biomass and composition are levelling off (Phillips et al., 2008, 2013), probably as a result of self-shading. Multiple lines of evidence in our study suggest that the phosphorus threshold for cyanobacterial blooms exceeding $1\,mm^3\,L^{-1}$ (corresponding to WHO low-risk threshold; Section S5) is $10–20\,\mu g\,TP\,L^{-1}$ in clear stratified lakes and $20–30\,\mu g\,L^{-1}$ in mesohumic stratified lakes, corroborating results from other studies (Carvalho et al., 2013; Derot et al., 2020; Vuorio et al., 2020). The TP target in clear stratified lakes should therefore not exceed $20\,\mu g\,L^{-1}$. Such a low threshold ($9\,\mu g\,TP\,L^{-1}$) has been implemented in Norwegian legislation for deep lakes characterized by low alkalinity, high water transparency, and stable summer stratification (Norwegian Classification Guidance, 2018). The higher TP threshold where cyanobacterial blooms may arise in brownwater lakes justifies slightly higher admissible TP targets without compromising the objectives of the EU WFD. However, in most EU countries, current TP targets (permissible concentrations) are much higher, up to $100\,\mu g\,L^{-1}$ (Kelly et al., 2021; Lyche Solheim et al., 2020; Phillips & Pitt, 2016). Clearly, more stringent TP targets and nutrient reduction measures to meet those targets are needed to protect stratified clearwater lakes from toxic cyanobacterial bloom formation.

Climate-proofing of lake management requires considering also other aspects than P thresholds, such as hypolimnetic oxygen depletion promoted by high temperatures and prolonged stratification periods, with negative impacts on zooplankton, benthic fauna and fish (Brothers et al., 2014); phosphorus and methane release from sediments as a result of anoxia (Bartosiewicz et al., 2021; Knoll et al., 2018); or the role of N availability in controlling cyanobacteria biomass and cyanotoxin production (Gobler et al., 2016; Hellweger et al., 2022; Litchman, 2023). Furthermore, for brownwater lakes attention is needed to reduce the risk of other harmful algal blooms, such as the rapidly spreading, skin irritating *Gonyostomum semen*, which tends to be favoured by nutrients and browning (Hagman et al., 2020), especially if high concentrations of iron (and Mn) contribute to the brown color (Lebret, Östman, et al., 2018). Thus, the combination of nutrient and climate change-related stressors (global warming and more frequent summer storms) will require tailored nutrient management schemes to reduce the risk of cyanobacterial bloom formation in lakes (Huisman et al., 2018; Reinl et al., 2023; Sterner, Reinl, et al., 2020).

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in Zenodo (Vansjø-dataset: https://zenodo.org/record/8392475); (WISER dataset: https://zenodo.org/record/8392818), and in FRED (Enclosure experiments dataset: https://doi.org/10.18728/igb-fred-843.0).

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