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Cyanobacteria can benefit from freshwater salinization following the collapse of dominant phytoplankton competitors and zooplankton herbivores

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Abstract

1. Freshwater salinization is an increasing threat to lakes worldwide, but despite being a widespread issue, little is known about its impact on biological communities at the base of the food chain.

2. Here we used a mesocosm set-up coupled with modern high-frequency sensor technology to identify short- and longer-term responses of phytoplankton to salinization in an oligotrophic lake. We tested the effects of salinization over a gradient of increasing salt concentrations that can be found in natural lakes exposed to road salt contamination (added salt range: from 0 to 1500 mg Cl⁻ L⁻¹).

3. The high-frequency chlorophyll-*a* (chl-*a*) fluorescence measurements showed an increasing divergence of chl-*a* concentrations along the salinization gradient over time, with substantially lower concentrations at higher salt levels. At the sub-daily scale, we found a profound suppression of day–night signal cycles with increasing salinity, which could be related to physiological stress due to the impairment of photosynthesis via effects on the photosystem II or potential changes in the active migration of phytoplankton. Community analyses revealed a similar decline pattern for the total phytoplankton biomass and a collapse of the total zooplankton biomass. Interestingly, we found a loss of phytoplankton diversity coupled with a compositional re-organization involving the loss of dominant green algae but increased biomass of salt-tolerant cyanobacteria.

4. Altogether, these results suggest that specific cyanobacterial taxa can benefit from freshwater salinization following the collapse of dominant phytoplankton competitors and zooplankton herbivores. The results also highlight the value of autonomous sensor technology to capture novel, small-scale ecological responses to freshwater salinization, and thereby to track fast changes in primary producer communities.

KEYWORDS
biodiversity, cyanobacteria, lakes, phytoplankton, salinization

1 | INTRODUCTION

Many freshwater ecosystems around the globe are increasingly experiencing salt pollution (Cañedo-Argüelles, 2020; Kaushala et al., 2018). The most documented drivers behind freshwater salinization are agriculture intensification, land clearing and resource extraction (Cañedo-Argüelles, 2020; Williams, 2001) as well as the use of deicing salts in cold geographical regions (Cunillera-Montcusí et al., 2022). Aquatic organisms usually have the capacity to withstand physiological stress caused by salinity changes, through, for example, osmoregulation, but only within a certain range (Bradley, 2009). Beyond a critical threshold for adaptation, vulnerable populations can collapse and become severely reduced or even locally extinct (Hintz & Relyea, 2019). Surpassing critical salinity thresholds can therefore have major consequences for conservation of aquatic biodiversity and the associated ecosystem services provided by freshwater bodies.

Over recent years, the threat that salinization poses to freshwater biodiversity has attracted substantial attention from the scientific community (Herbert et al., 2015; Hintz & Relyea, 2019). Yet, we still know little about the responses of biological communities at lower trophic levels, especially on primary producers, such as phytoplankton, both in terms of functional and compositional dynamics (but see, e.g. Astorg et al., 2022; Ersoy et al., 2022; Fournier et al., 2021, 2022; Hintz et al., 2017; Moffett et al., 2020; Sim et al., 2006; Strehlow et al. 2005). Phytoplankton are crucial primary producers in aquatic systems (Behrenfeld et al., 2009), as their growth and community composition are strong determinants of energy and matter transfer efficiency to higher trophic levels, such as zooplankton or macroinvertebrates and which then serve as food to other consumers such as fish and amphibians (Striebel et al., 2008, 2012; Thomas et al., 2022). Some phytoplankton taxa, such as cyanobacteria, can also endanger substantially water quality for both humans and aquatic organisms due to the production of a wide range of toxins (Codd, 1995). Moreover, cyanobacteria can constrain the transfer of energy within the food web due to their low nutritional quality for consumers such as crustacean zooplankton (Ger et al., 2016). Hence, it is important to further broaden our understanding of the responses of natural phytoplankton communities to salinization, as changes in their biomass and composition will have cascading effects across trophic levels, as well as on critical ecosystem services, such as drinking water supply or recreational use, among many others (for a review on ecosystem services provided by phytoplankton, see Naselli-Flores & Padisák, 2023).

Comprehensive studies on this topic across 16 sites in North America and Europe revealed an overarching negative response across zooplankton population abundances and divergent (positive or negative) responses of phytoplankton biomass using chlorophyll-*a* (chl-*a*) concentrations as a proxy (Arnott et al., 2022; Hébert et al., 2022; Hintz et al., 2022). While these patterns suggest that phytoplankton blooms can increase, decrease or remain stable as a function of each site-specific abiotic and biotic context, it remains largely unknown whether similar functional patterns (i.e. biomass dynamics) would emerge using other aggregated indicators at the

community level (e.g. community biomass estimates based on microscopic counts) than chl-*a* concentrations. Chl-*a* concentrations as biomass proxy alone should be taken with caution, as adaptation mechanisms to environmental change can lead to the upregulation of chl-*a* (the increase at the cellular level of the amount of chl-*a*) and thereby decouple their positive correlation with the phytoplankton standing stock (Alvarez-Fernandez & Riegman, 2014; Urrutia-Cordero, Langenheder et al., 2021). Moreover, different single-site studies have shown that halotolerant members of, for example, the Chrysophyceae (golden algae), Cryptophyceae or Cyanophyceae classes can benefit from increasing salt concentrations based on molecular eDNA analyses (Astorg et al., 2022; Fournier et al., 2021, 2022). These results indicate that phytoplankton communities, just like zooplankton, might suffer a strong compositional reorganization upon salinization.

To improve our understanding of phytoplankton functional (biomass standing stock) and biodiversity responses to salinization over a range of time scales (c.f. Marce et al., 2016, Urrutia-Cordero, Langvall et al., 2021), we conducted a mesocosm experiment using a wide range of methodologies, including standard microscopy and analyses of chl-*a* pigments as a proxy for phytoplankton biomass, as well as high-frequency sensor technology based on chl-*a* fluorescence measurements. Our experiment was conducted in the oligotrophic waters from a shallow hemiboreal lake and was designed to mimic the effects of a pulse of sodium chloride as a de-icing agent used for roads and urban areas in boreal and hemiboreal regions (Cunillera-Montcusí et al., 2022). We tested the following two main hypotheses:

> **Hypothesis 1.** Increasing salt concentrations reduce the total phytoplankton biomass over time. Salt pollution in freshwater systems can reduce the survival, growth and reproduction of many animal and plant organisms (e.g. macrophytes, zooplankton, macroinvertebrates, amphibians, fish; Hintz & Relyea, 2019), and so we expect a similar response in phytoplankton at the community level resulting in an overall reduction in phytoplankton biomass.

> **Hypothesis 2.** The decline in total phytoplankton biomass is followed by a reduction in taxa richness (potential local extinctions) and changes in community composition, including shifts in dominance to some salt-tolerant taxa. We expect some salt-tolerant taxa to persist and to compensate to some extent for the decline in total phytoplankton biomass due to the loss of sensitive taxa (e.g. see McClymont et al., 2023). In fact, other studies often observed an increase in total phytoplankton biomass facilitated by lower top-down control due to the concomitant collapse of crustacean zooplankton communities in response to salinization (Hintz et al., 2022). However, as phytoplankton in oligotrophic lakes (as in our tested system) are often nutrient-limited, we do not expect an increase in total

phytoplankton biomass following the decline in top-down control by zooplankton.

2 | METHODS

2.1 | Study design

The experiment was conducted using the SITES-AquaNet infrastructure (Urrutia-Cordero, Langvall et al., 2021) in Lake Feresjön (SITES Asa Research Station). Lake Feresjön is an oligotrophic lake (area = 0.45 km², maximum depth = 13 m, mean depth = 4 m) located in a forest-dominated catchment in Southern Sweden (N° 57.180, E° 14.805), with the chl-*a* and total phosphorus mean annual concentrations of 1.7 and 7.1 µg L^{-1}, respectively (see Urrutia-Cordero, Langvall et al., 2021; Urrutia-Cordero, Langenheder et al., 2021 for more information). The experiment ran for 6 weeks, from 3 July to 14 August 2018. The experiment consisted of 20 cylindrical, polyethylene enclosures that were used as mesocosms (diameter = 0.9 m; height = 1.5 m; volume = 700 L; Cipax AB). The mesocosms were submerged in the lake (except the upper 30 cm) and stabilized with ropes to a jetfloat (Jetfloat International GmbH). Each mesocosm was filled with 550 L of lake water (depth ~ 1 m) using a centrifugal water pump (Meec tools 735-018, JULA AB) with an inner diameter of 48 mm of the tube. To minimize the variation of the zooplankton community across mesocosms, the water was pumped through an 80-µm nylon mesh to exclude large-bodied zooplankton. The filtered zooplankton was collected in a tank with 40 L of lake water, mixed and aliquots from this tank then served as an inoculum for each mesocosm. It is important to note that any potential phytoplankton taxa that were retained in the 80 µm nylon mesh were also present in this zooplankton inoculum. To enhance the amount of zooplankton, we filtered about twice as much water from the lake as was needed to fill up the mesocosms, and the collected zooplankton were added proportionally to each mesocosm to ensure achieving a well-established initial zooplankton community with a density of 18 ± 5 individuals L^{-1} (average ± SD) in the mesocosms. After filling the mesocosms, the communities were allowed to establish for 5 days before starting the experimental manipulations.

The experimental design consisted of a gradient of increasing salt concentrations (20 mesocosms representing 20 chloride concentrations. Added salt range: from 0 to 1500 mg Cl⁻ L^{-1}). The achieved gradient (actual salt concentrations; Figure S1 in the Appendix) covered chloride levels that can be found in natural lakes exposed to road salt contamination (Dugan et al., 2017; MacLeod et al., 2011; Sibert et al., 2015). Chloride concentrations in lakes due to natural sources typically range between 0 and 10 mg L^{-1} (Kelting et al., 2012; MacLeod et al., 2011). The mesocosms were randomized within the jetfloat prior to the start of the experiment. Each mesocosm received different amounts of salt (NaCl with a purity of >99%) according to their respective assigned nominal Cl⁻ additions. The salt was added to the mesocosms dissolved in distilled water, and then the mesocosms were mixed to ensure a homogenous salt distribution in each enclosure. Background chloride concentrations prior to salt additions were low (mean ± SD across all mesocosms: 6.61 ± 0.06 mg L^{-1}) compared to the variation generated along the gradient after the salt addition. There were only small differences between the nominal and measured chloride concentrations along the gradient (Figure S1 in the Appendix). To maintain the same chloride concentrations in the mesocosms throughout the experiment, the liquid volume in the mesocosms was adjusted after samplings by adding distilled water to compensate for evaporation losses. Chloride analytical methods in both lake and mesocosms are described below.

2.2 | Sensor technology

We used autonomous sensor fluorescence technology to provide a comprehensive view of phytoplankton response patterns to freshwater salinization across multiple temporal scales. Autonomous high-frequency sensors reduce the risk of distorting the continuous nature of response variables (c.f. "temporal aliasing"; Marce et al., 2016; Shannon, 1948), while having the potential to capture small-scale ecological phenomena that occur within the sub-daily scale (Marce et al., 2016; Urrutia-Cordero, Langvall et al., 2021), including day–night fluctuations in chl-*a* fluorescence that relate to changes in photosynthetic performance (Rousso et al., 2021).

We recorded high-frequency chl-*a* fluorescence (reported as chl-*a* concentrations by the sensor output) using 17 available TriLux fluorometers (Chelsea Technologies Group). We deployed one fluorometer in each mesocosm at a depth of 60 cm, except for three mesocosms, as the amount of available TriLux sensors was limited to 17. The excluded nominal chloride concentrations were 20, 60 and 800 mg L^{-1}, which were selected to minimize the limitations of analyses over the full range of salinization that could be performed when not all levels could be included. The fluorometers were connected to a Campbell CR1000 datalogger (Campbell Sci). Sensors were requested for readings every 1 min through an SDI-12 communication protocol (Urrutia-Cordero, Langvall et al., 2021). At that time, communication between the datalogger and the sensors only had a success rate of approximately 50%; that is, the sensors answered only about half of the requests and, thus, delivered only about 30 sensor readings per hour. After data quality management (see Appendix S2), hourly chl-*a* concentration was calculated as the average of all available minute data recorded within each hour (i.e. on average about 30 values), as no significant patterns in any shorter frequency were found. Communication with the sensors was successfully established on experimental day 17. Hence, we present data from experimental days 17–42.

2.3 | Sampling and sample analyses

Mesocosm water samples were also collected three times in total, on experimental day 0 (prior to the experimental manipulations, i.e. 3 July), day 21 (24 July) and day 42 (14 August, i.e. at the end of the

experiment). We collected samples for the determination of phytoplankton biomass and community composition. Before sampling, the water in each mesocosm was mixed thoroughly with a rod with a flat disc at the bottom end. A total volume of 16 L water was then sampled with a Ruttner sampler (2 L), from two depths (5–45 and 45–85 cm below the water surface) in the 100-cm water column. Sampling was done from the sides of the mesocosms, half-way between the centre and the side wall, to avoid taking samples close to the wall and to avoid the pole with the sensors in the centre. The water collected was pooled in a 20-L bucket. After homogenization by mixing, sub-samples were collected in 100-mL glass bottles with Lugol's solution for the determination of phytoplankton biomass and community composition. Phytoplankton abundance and size estimations were obtained to the lowest possible taxonomic level (species, if not genus) using Utermöhl chambers (10 mL) and an inverted microscope according to Brierley et al. (2007). Biovolume estimates were obtained from abundance and size measurements based on Olenina et al. (2006) and converted into biomass estimates assuming a density of $1 \, g \, cm^{-3}$.

From the 16 L of water, we also took subsamples for chloride, nutrients and zooplankton (as a proxy for the top-down pressure on phytoplankton). For chloride and nutrient analyses, samples were sent to the Biogeochemical Analysis Laboratory at the Swedish University of Agricultural Sciences, where chloride concentrations were measured using an isocratic system with a conductivity detector (IC Metrohm Net ver. 2.3) and the method SS-EN ISO 10304-1 1st ed. (modified), and $N-NO_3$ and $P-PO_4$ were measured using spectrophotometric analyses (Autoanalyser AA3 from Omniprocess AB) using the SS-EN ISO 13395 method for $N-NO_3$ and the Bran*Luebbe method no. G-175-96 Rev. 15 (Multitest MT 18) for $P-PO_3$. Zooplankton samples were collected by filtering 10 L of water from the 16 L integrated water sample with a 50 µm nylon mesh. The animals collected on the mesh were then transferred to 100 mL glass bottles and fixed with Lugol's iodine. Zooplankton samples were counted to taxa level (counting cladocerans, copepods and rotifers) on an inverted microscope and biomasses were estimated using length–weight regressions (Bottrell et al., 1976; Dumont et al., 1975).

2.4 | Data analyses

First, our data analyses focused on determining the effect of salinization on the total phytoplankton biomass, as an indicator of the overall standing stock at the base of the food chain. Second, we explored whether there were changes in species richness, as an indicator of the potential local extinction of taxa as well as in community composition. Changes in the latter (community composition) were first explored by computing the temporal community turnover of phytoplankton. The turnover in phytoplankton composition was calculated based on Jaccard dissimilarity between salt-added treatments and the control within each sampling. Jaccard is based on presence–absence information of taxon identities,

and it is bound between 0 and 1, with 1 being the maximal dissimilarity (complete exchange of species identities relative to control conditions). Then, we focused on identifying changes in major functional phytoplankton groups and taxa to pinpoint which taxa benefited from or were unfavoured by salinization. At last, we also analysed the effects of salinization on the daily amplitude of the chl-*a* concentration based on fluorescence. We present these patterns because, after an initial exploration of the chl-*a* concentration temporal dynamics, we identified a strong disruption of day–light and night–dark concentration cycles with increasing salinity (i.e. day–night fluctuations in chl-*a* fluorescence, Figure 1), and these changes could be related to physiological stress due to the impairment of photosynthesis via effects on the photosystem II (see Discussion). To illustrate these day–night differences in fluorescence, we computed daily amplitudes calculated as the difference between the maximum concentration value recorded during the darkest period that occurs between two consecutive days (from 9.01 p.m. to 3.00 a.m. of the next day, when it is completely dark) and the minimum chl-*a* concentration recorded during the lighter following hours (from 3.01 a.m. to 9.00 p.m., daytime).

We used generalized additive models (GAMs) to evaluate whether the salinization gradient significantly explained across-mesocosm-variation of total phytoplankton biomass, daily amplitude of the chl-*a* concentration (based on high-frequency chl-*a* fluorescence measurements), phytoplankton species richness and turnover and biomass of susceptible phytoplankton classes. We used GAMs because of their flexibility and ability to capture nonlinear dynamics along the salinization gradient, as opposed to less versatile models such as linear regressions. Although the phytoplankton community was represented by 14 different classes, we only present statistically significant responses, which were found for the Zygnematophyceae and Cyanophyceae classes, which were the major dominant groups, eventually contributing up to 50% and 40% of the total phytoplankton biomass, respectively (Figure S2 in the Appendix). We also analysed responses of zooplankton biomass as well as nutrient concentrations (the latter can be found in the Figure S1 in the Appendix). All models were run for each sampling separately (beginning, middle and end of the experiment). All statistical analyses were done using R, version 4.0.0. GAMs were run using the 'gam' function (family: gaussian; link function: identity) from the 'mgcv' package.

3 | RESULTS

3.1 | Response of chlorophyll-*a* concentration to salinization

Chlorophyll-*a* concentrations decreased substantially along the salinization gradient in two distinctive ways (Figure 1). First, we observed a reduction of overall chl-*a* concentration with increased salinity, especially notable by the end of the experiment (Figure 1). Second, there was a strong suppression of the maximum
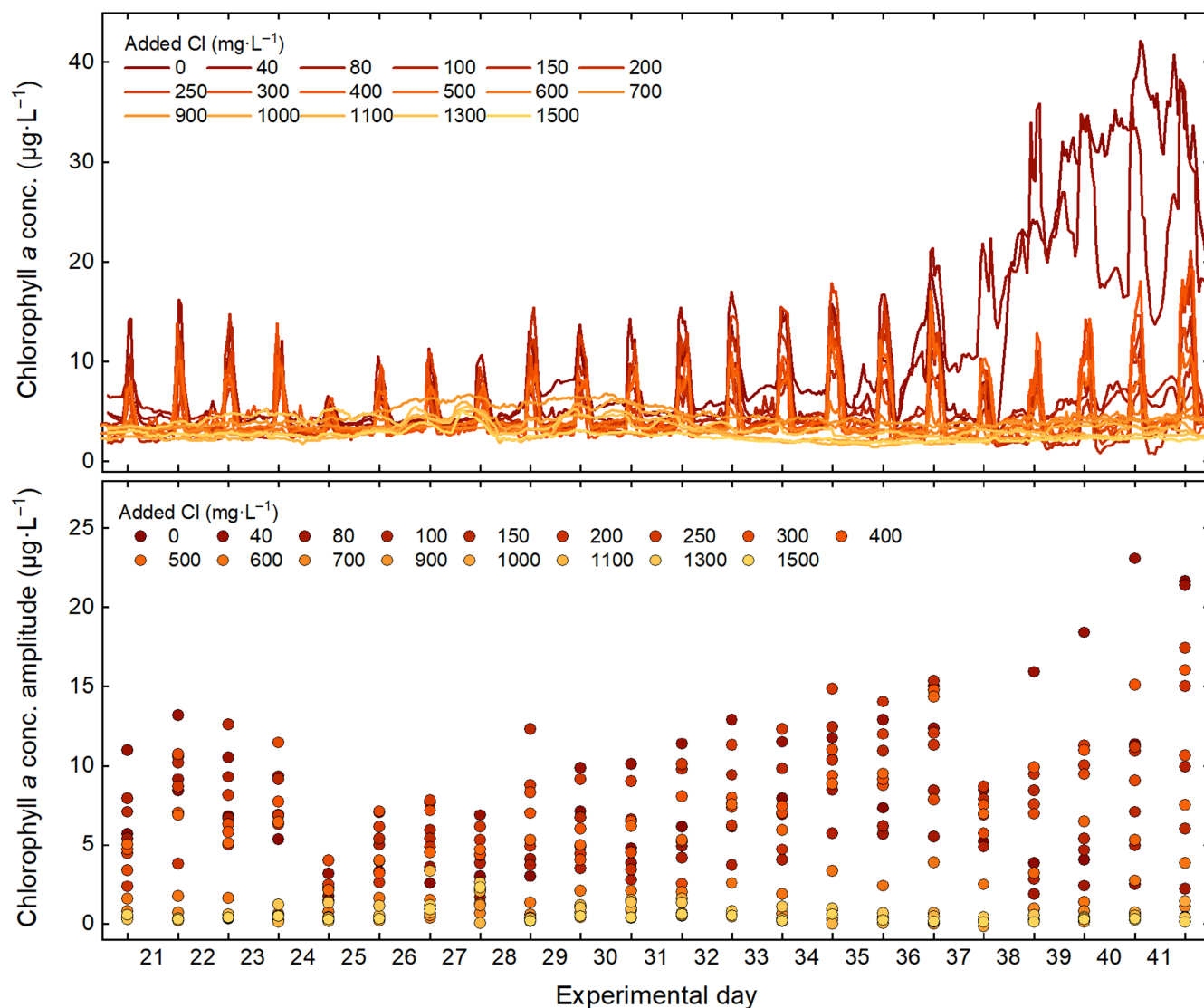
FIGURE 1 High-frequency chlorophyll-*a* (chl-*a*) concentration estimates from fluorescence measurements recorded during the experiment along the salinization gradient. Upper panel: hourly average of chl-*a* concentration ($\mu g\,L^{-1}$). Lower panel: daily chl-*a* concentration amplitude. Note that we only include amplitude estimations for days where there were complete measurements along the salinization gradient (i.e. since experimental day 21).

concentration with increased salinity, which consistently occurred during the darkest period of each day (Figure 1). Consequently, we found a significant salt effect (Table 1, $p < 0.001$) with a reduction of daily chl-*a* concentration amplitudes with increasing salinity over the entire recorded period (Figure 1).

3.2 | Response of the phytoplankton community to salinization

On average across all mesocosms (including those with no salt addition), we observed that the total phytoplankton biomass decreased about more than twofold from the start to the end of the experiment (Figure 2). We did not observe any change in biomass along the salinization gradient at the mid-sampling (3 weeks after salt additions; Figure 2 and Table 1). However, the total phytoplankton

biomass gradually decreased until a nominal salt concentration of 400 mg Cl⁻ L⁻¹ at the final sampling (6 weeks after salt additions), a salinity threshold above which the biomass production had halved and remained steady until the highest nominal salt concentration (of 1500 mg Cl⁻ L⁻¹) (Table 1, $p = 0.043$). In parallel, we observed a significant reduction in species richness along the salinization gradient at the end of the experiment (Figure 2 and Table 1, $p = 0.007$). The total number of species decreased by half until a nominal salt concentration of 400 mg Cl⁻ L⁻¹, a salt effect that was constant for higher nominal salt concentrations except for a slight upward trend driven by the mesocosm with the highest nominal salt concentration (Figure 2).

Our analyses also revealed a notable increase in the turnover of species identities with increasing salt concentrations (Figure 2). The trend of observed changes in community composition was already visible after 3 weeks of salt additions (Table 1, marginally non-significant salt effect, $p = 0.067$), a pattern that remained constant

TABLE 1 Generalized additive models evaluating whether the salinization gradient significantly explained variation in the analysed response variables at experimental days 0 (start), 21 (middle) and 42 (end).

Response variable	Sampling	n	R^2 (adj)	Deviance explained (%)	Ref. df	F-value	p-Value
Chl-a daily amplitude	Middle	17	0.67	71	2	8.40	**<0.001**
	End	17	0.51	54	1	17.67	**<0.001**
Total phytoplankton biomass	Start	20	0.05	10	1	1.56	0.205
	Middle	20	−0.01	7	2	0.25	0.627
	End	20	0.38	49	4	3.18	**0.043**
Species richness	Start	20	−0.01	4	1	0.74	0.401
	Middle	20	−0.02	3	1	0.52	0.478
	End	20	0.57	67	5	4.79	**0.007**
Compositional turnover	Start	19	−0.04	2	1	0.35	0.563
	Middle	19	−0.26	33	2	3.17	**(0.067)**
	End	19	0.43	54	4	3.34	**0.032**
Zygnematophyceae biomass	Start	20	−0.03	3	1	0.50	0.487
	Middle	20	0.38	44	2	5.38	**0.013**
	End	20	0.609	69	4	6.42	**0.003**
Cyanophyceae biomass	Start	20	−0.05	1	1	0.10	0.759
	Middle	20	0.53	59	3	7.45	**0.002**
	End	20	0.71	78	5	8.42	**<0.001**
Total zooplankton	Start	17	−0.04	2	1	0.29	0.598
	Middle	17	0.94	95	3	91.61	**<0.001**
	End	17	0.91	92	1	132.20	**<0.001**

Note: Black-bolded p-values denote significant effects of the explanatory variable ($p \leq 0.05$), whereas black-bolded p-values in brackets denote marginally significant effects ($0.5 < p < 0.1$).

until the end of the experiment when it finally was found to be significant (Table 1, $p = 0.032$).

3.3 | Responses of dominant phytoplankton groups

The Zygnematophyceae class was one of the most dominant phytoplankton groups in mesocosms that received none or little salt additions. Thus, in these mesocosms, this group largely contributed (about 50%) to the total phytoplankton standing stock (Figure S2 in the Appendix). The group of Zygnematophyceae showed a significant gradual biomass decline along the salinity gradient after 3 weeks (Figure 3 and Table 1, $p = 0.013$) and became almost extinct by the end of the experiment in mesocosms above 400 mg Cl$^-$ L^{-1} (Figure 3 and Table 1, $p = 0.003$). These patterns were mainly driven by a biomass decline in the dominant genus *Mougeotia* (Figure S3 in the Appendix).

The Cyanophyceae class profited substantially from the addition of salts, becoming a dominant group (about 30–40% of the total phytoplankton biomass) at the highest salt levels by the end of the experiment (Figure S2 in the Appendix). Cyanobacteria already showed a significant increase in biomass with elevated salt concentrations 3 weeks after salt additions (Figure 3 and Table 1, $p = 0.002$). The positive effect of salt additions on cyanobacterial biomass was even more pronounced at the end of the experiment (Table 1, $p < 0.001$), when the biomass had increased by about sixfold along the entire gradient (Figure 3). These patterns were mainly driven by a biomass increase in the genus *Planktolyngbya* (Figure S3 in the Appendix).

3.4 | Response of the zooplankton community to salinization

The zooplankton community was strongly affected by salt additions, with clear effects already at low-to-moderate salt levels (Figure 4). The total zooplankton biomass significantly declined with increasing salt concentrations after 3 weeks of the experiment (middle sampling), thus becoming almost negligible above 700 mg Cl$^-$ L^{-1} (Figure 4 and Table 1, $p < 0.001$). A similar, but stronger pattern was observed at the end of the experiment when no zooplankton was found above 800 mg Cl$^-$ L^{-1} and onwards (Figure 4 and Table 1, $p < 0.001$). Before the start of the experimental manipulations, the zooplankton community was dominated (on a biomass basis) by cyclopoid copepods and nauplii (>80% contribution to the total zooplankton biomass across all mesocosms), but by the mid-to-end sampling, they only occurred in mesocosms below 400 Cl$^-$ L^{-1} (Figure S4 in the Appendix). Cladocerans, mainly *Bosmina*, were dominating (although at low absolute biomass levels) in salt addition treatments above 300 Cl$^-$ L^{-1} and were one of the only taxa that were present above 400 Cl$^-$ L^{-1} (Figure S4 in the Appendix). Rotifers made a minor contribution to the total zooplankton biomass throughout the experiment (Figure S4 in the Appendix).

4 | DISCUSSION

The results of this study suggest that certain cyanobacterial taxa can benefit from multi-trophic functional and biodiversity change caused by salinization in oligotrophic freshwater. First, we can
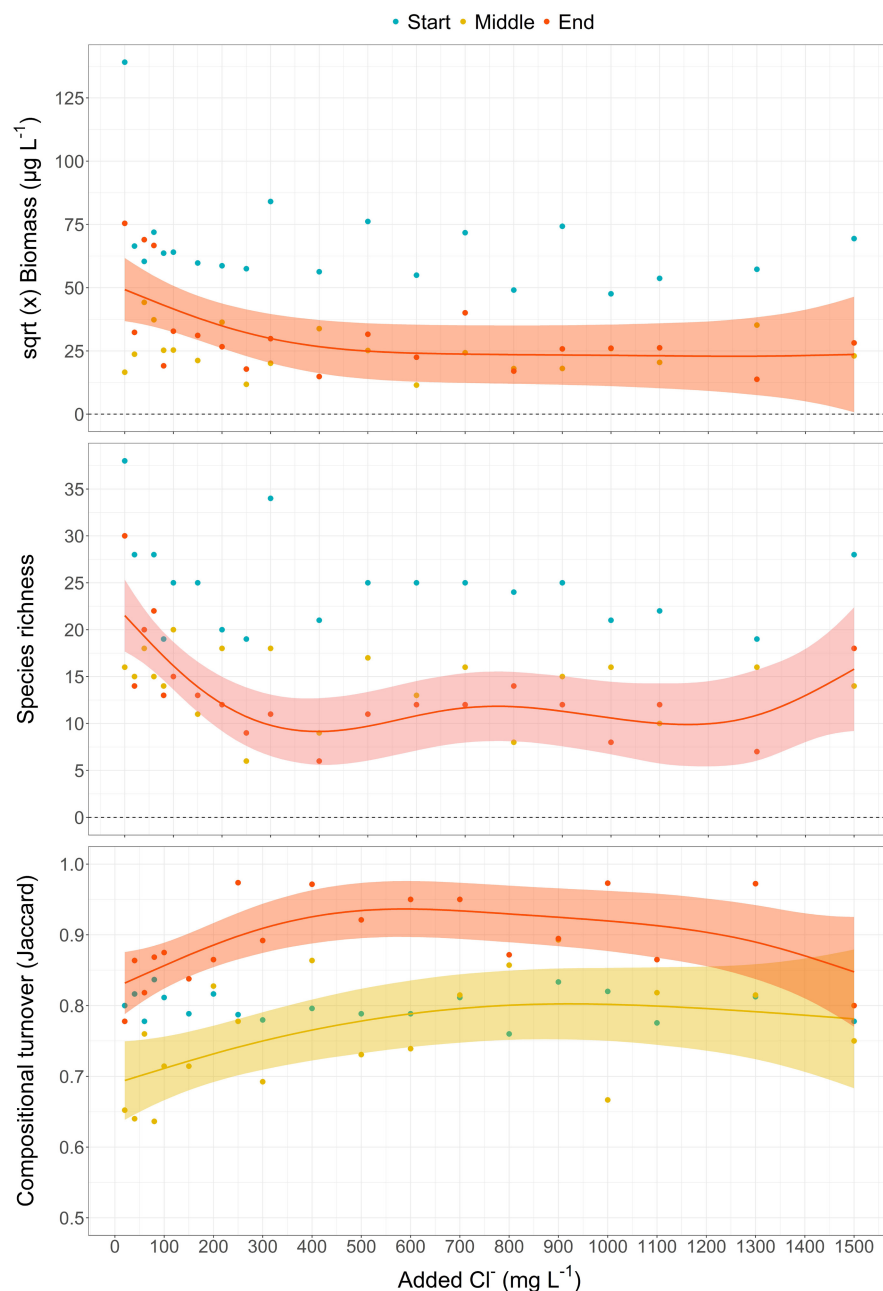
FIGURE 2 Total phytoplankton biomass (sqrt transformed), species richness and compositional turnover of phytoplankton community responses along the salinization gradient. Blue, yellow and red symbols represent the start (experimental day 0, prior salt additions), middle (day 21) and end (day 42) samplings. Fitted GAMs with CI (95%) are shown for samplings where there was a significant ($p < 0.05$) or marginally non-significant ($p < 0.1$) association between response variable and added chloride concentrations (see Table 1). CI, confidence interval; GAM, generalized additive model.

corroborate H1 as we could show that the phytoplankton community halved their standing stock (total biomass) already at about 400 mg Cl⁻ L⁻¹ chloride concentration (and onwards) after 6 weeks of exposure time in congruence with the decline in the total zooplankton biomass (Figure 4). No changes in total phytoplankton biomass were observed in mid-term samples, which suggests that susceptible phytoplankton species can cope with high salinity levels for a certain time frame, as many taxa possess various osmoregulatory mechanisms, such as carbohydrate and protein syntheses (e.g. see Abid et al., 2008; Rosen et al., 2018). Interestingly, our results also reveal that the reduction in total phytoplankton biomass was accompanied by a strong compositional re-organization (corroborating H2). The total number of species halved already at relatively moderate nominal salt concentrations (400 mg Cl⁻ L⁻¹), including the loss of dominant green

algal taxa, such as *Mougeotia* from the Zygnematophyceae class. The winners from these changes were halotolerant cyanobacterial taxa such as *Planktolyngbya*. Overall, the total cyanobacterial biomass increased sixfold along the entire salinization gradient by the end of the experiment. The observed changes occurred at environmentally relevant salt concentrations that may occur after salt pulses of sodium chloride used as deicing agents for roads and urban areas in boreal and hemiboreal regions (Cunillera-Montcusí et al., 2022), with important implications for the functioning of lakes and biodiversity conservation.

Cyanobacterial taxa, such as *Planktolyngbya* grow in filaments, which like many other cyanobacteria that also grow in filaments or colonies, reduce the possibility for herbivorous zooplankton to ingest them (Ger et al., 2016; Urrutia-Cordero et al., 2015, 2016). In addition, some cyanobacteria often produce toxic compounds and possess low

FIGURE 3 Biomass responses of susceptible phytoplankton groups (i.e. sqrt transformed total Zygnematophyceae biomass and total Cyanophyceae biomass) to increasing salt concentrations. Blue, yellow and red symbols represent the start (experimental day 0, prior salt additions), middle (day 21) and end (day 42) samplings. Fitted GAMs with CI (95%) are shown for samplings where there was a significant ($p < 0.05$) association between response variable and added chloride concentrations (see Table 1). CI, confidence interval; GAM, generalized additive model.
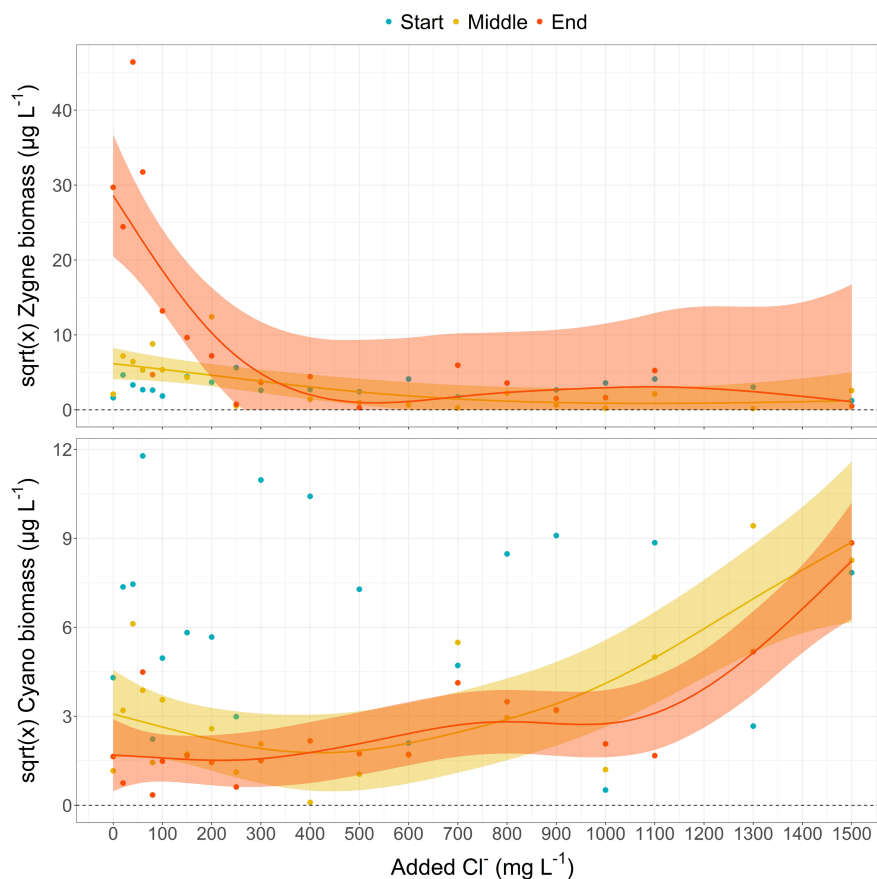
nutritional values (fatty acids) reducing the growth and fitness of herbivore communities (Ger et al., 2016; Urrutia-Cordero et al., 2013). Specifically, *Planktolyngbya*-isolated strains have shown their ability to produce cyanotoxins, such as the potent hepatotoxic microcystins (Pineda-Mendoza et al., 2012). All these factors constrain the transfer of energy and matter to higher trophic levels, which may be especially relevant in oligotrophic lakes where there often exist trophic bottlenecks caused by nutrient limitation (Sterner, 2008). Hence, higher trophic levels (zooplankton, amphibians, fish and others) may not only suffer from the direct effects of salinization (Cunillera-Montcusí et al., 2022) but also from compositional changes at the bottom of the food web. Moreover, cyanobacteria are the primary taxa causing toxic freshwater algal blooms in eutrophic lakes, which pose a considerable risk to human health as well (Codd et al., 2005; Urrutia-Cordero et al., 2013), and which may be exacerbated given that salinization can cause the leakage of intracellular toxins (microcystins) out from the cells due to the loss of membrane integrity (Rosen et al., 2018). Other studies have reported the persistence of *Planktolynbya* species under salt stress in systems suffering from salt intrusion (Marshall, 2012), and studies conducted in Canada have also shown that other potentially harmful cyanobacterial taxa (*Dolichospermum* or *Pseudoanabaena*) can benefit from salinization (Fournier et al., 2021, 2022). Mucilage production can serve as a mechanism to protect the cell viability of bloom-forming filamentous and colony-forming cyanobacteria under salt stress (Rosen et al., 2018). It is therefore important to further investigate the generality of these results and whether they hold across more lake types, especially for potential toxic-bloom-forming taxa in eutrophic lakes. The outcomes of salinization with regards to phytoplankton diversity change might also be context-specific, as other halotolerant taxa (e.g. Ochrophyta or Cryptophyta) have been shown to profit from increasing salt concentrations (Astorg et al., 2022; Fournier et al., 2021, 2022). These different results pose the question of whether the same phytoplankton taxa tend to experience the same dynamics and responses to salinization across the globe. Coordinated distributed experiments offer great potential to evaluate salinization effects on phytoplankton community dynamics as has already been demonstrated for zooplankton, both related to specific results from single-site studies and overarching patterns emerging across geographically distant lakes (Arnott et al., 2022; Hébert et al., 2022; Hintz et al., 2022).

It is important to stress that we observed a 50% reduction in zooplankton biomass (in a community initially dominated by cyclopoid copepods and *Bosmina*) at concentrations of 300–400 mg Cl⁻ L⁻¹ already after 3 weeks of exposure, and that the zooplankton biomass became almost negligible above 700–800 mg Cl⁻ L⁻¹. The reduction in zooplankton biomass has been shown to putatively increase phytoplankton blooms in certain cases (Hintz et al., 2022). However, members of the Cladocera sub-order like *Bosmina* or cyclopoid copepods (which dominated in our experiment) are generally small-sized taxa and display modest or minor consumption rates on large-size filamentous or colonial cyanobacteria (Ger et al., 2016; Urrutia-Cordero et al., 2015). Hence, we expect that the loss of these zooplankters only contributed to a minor extent to the increase in cyanobacterial biomass at high salt concentrations.
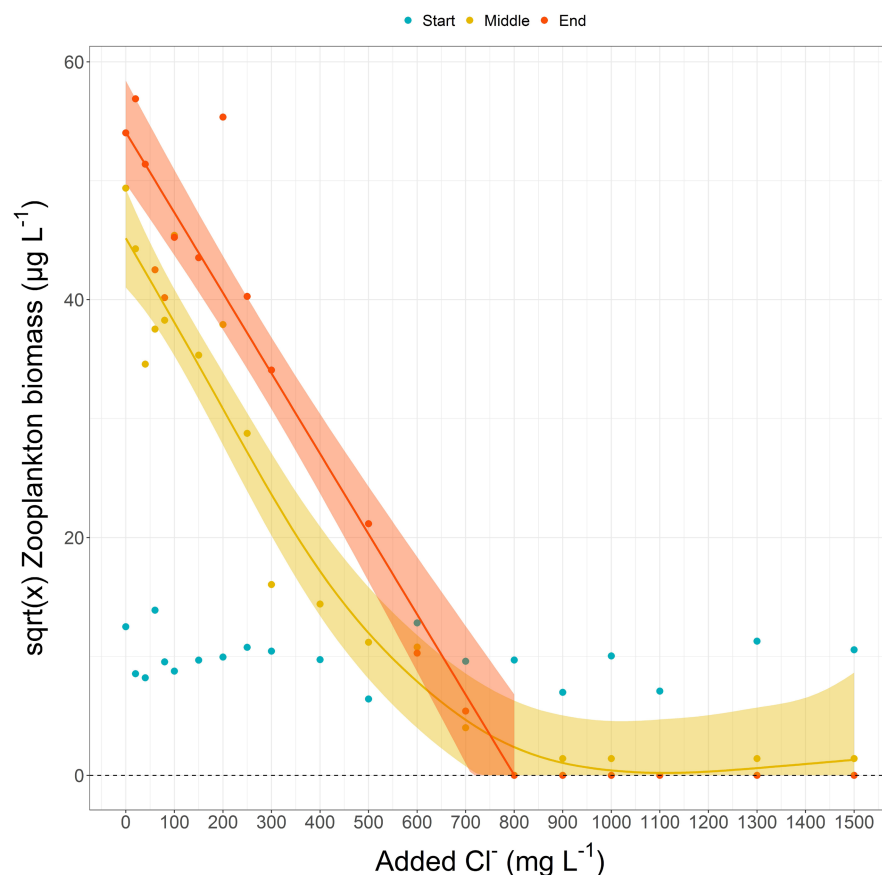
FIGURE 4 Total zooplankton biomass (sqrt transformed, µg L⁻¹) along the salinization gradient. Blue, yellow and red symbols represent the start (experimental day 0, prior salt additions), middle (day 21) and end (day 42) samplings. Fitted GAMs with CI (95%) are shown for samplings where there was a significant ($p < 0.05$) association between response variable and added chloride concentrations (see Table 1). CI, confidence interval; GAM, generalized additive model.

Our results also show novel ecological phenomena at the sub-daily scale, involving a profound suppression of day–night chl-*a* fluorescence signal cycles (expressed as chl-*a* concentrations) with increasing salinity. To our knowledge, this is the first study showing such phytoplankton response patterns to freshwater salinization at the community level, or any other stressor type that affects photosynthetic performance (e.g. temperature, nutrients, pH or other pollutants). Although this hypothesis remains to be tested, such signals may be an indication of physiological stress from PSII damage to salt additions, in a similar way as terrestrial plants and phytoplankton cultures in the lab have been shown to respond to physiological stress due to increasing salinity (Lu & Vonshak, 2002; Najar et al., 2018; Tiwari et al., 1998; Tsai et al., 2019).

In general, studies with primary producers have shown that the light absorbed by chlorophyll molecules takes one of three pathways: (1) photosynthesis (photochemical pathway), (2) dissipation of excess energy as heat (non-photochemical pathway) or (3) emission as light of longer wavelength compared to that of the absorbed light (fluorescence pathway) (Maxwell & Johnson, 2000). A sudden light pulse, such as one emitted by a fluorometer during night when phytoplankton are in a 'dark-adapted state' progressively 'closes' PSII reaction centres which absorb light and transfer electrons to a downstream electron acceptor (quinone Qa) within the photochemical pathway process. The 'closure' of these action centres is compensated by increasing the yield of fluorescence via the fluorescence pathway and leads to a higher chl-*a* fluorescence signal during the 'dark-adapted state' compared to a 'light-adapted state'. While this light-induced fluorescence quenching mechanism, which is responsible for the day–night

fluorescence fluctuations observed in our study (Figure 1), has already been shown to occur for phytoplankton (Rousso et al., 2021), the most remarkable and novel aspect of our results is the loss of the fluorescence peak during night with increasing salt concentrations. Those patterns occurred since the first chl-*a* fluorescence measurements (Figure 1) and were likely driven by the damage and inability of PSII to absorb energy, which is why those signals are commonly used as an indicator of stress in terrestrial plants (including salinity; Maxwell & Johnson, 2000). At the molecular level, the ionic effect of increasing salinity is likely caused by an increased influx of Na+ ions through potassium/Na+ membrane channels, which in turn increase concentrations of salts in the cytosol and irreversibly inactivate PSII activity (Allakhverdiev et al., 2000). These ionic effects have been studied in the laboratory with both eukaryotic and prokaryotic phytoplankton (Allakhverdiev et al., 2000; Demetriou et al., 2007), and there seems to be species inter-specific differences in stress and adaptive responses through changes in the functional size of the antenna and density of active photosystem II reaction centres (Demetriou et al., 2007).

To specifically test the hypothesis that increasing salt stress disrupts the photosynthetic pathway, future studies with complex phytoplankton communities could use AM fluorometry (Maxwell & Johnson, 2000), which is a common technique to study the potential damages of PSII in primary producers. It is also important to acknowledge that the photosynthetic performance of prokaryotes and eukaryotes is different (Schuurmans et al., 2015), and that different patterns could emerge between phytoplankton communities dominated by eukaryotic or prokaryotic phytoplankton. Moreover, sensor

measurements in our mesocosms were set at the same depth (60 cm), so we cannot rule out that the observed day–night variation in fluorescence in the control mesocosm is explained (at least partly) by active migration of some phytoplankton taxa. Hence, it is also worth exploring further whether the suppression of those night chl-*a* fluorescence peak signals with increasing salinity is partly driven by changes in the active migration of some phytoplankton taxa within the mesocosms.

At last, it is important to remark that the described reduction in total phytoplankton biomass at the end of the experiment matched well with the observed reduction in daily average chl-*a* fluorescence signals (expressed as chl-*a* concentrations, Figure 1) (Pearson's correlation: $r = 0.85$, $p < 0.001$). However, chl-*a* pigment concentrations estimated from chl-*a* extracted from collected filters were not a reliable predictor of the total phytoplankton biomass (Pearson's correlation; $r = 0.03$, $p > 0.89$). In fact, these chl-*a* pigment concentrations showed an opposite pattern as the total phytoplankton biomass and chl-*a* concentration measured with the fluorometers at the end of the experiment, showing a significant increasing trend along the salinization gradient (Table 1 and Figure S6 in the Appendix). One potential cause for the observed mismatch is that phytoplankton attempted to compensate for the induced salt stress by upregulating more chl-*a* pigments, a mechanism observed sometimes in terrestrial plants (Lacerda et al., 2006). Another possible explanation is that the observed compositional reorganization of the phytoplankton community resulted in an increased dominance of taxa characterized by higher pigment content per biomass unit (Marzetz et al., 2020). Regardless of the mechanism behind these patterns, the observed decoupling between the total phytoplankton biomass (measured from microscopic counts) and chl-*a* pigment concentrations suggest that future studies on freshwater salinization should use various proxies of the phytoplankton standing stock, thus not only relying on chl-*a* concentrations as most used.

We conclude that freshwater salinization can reduce both phytoplankton biomass and biodiversity at the community level in shallow oligotrophic waters. We found these changes to be accompanied by a strong community reorganization, with a decline in dominant green algae (*Mougeotia* from the Zygnematophyceae class) and an increase in salt-tolerant cyanobacteria (*Planktolyngbya*). Hence, our results open up new questions related to the potential disruption of trophic interactions and energy flow in shallow oligotrophic, boreal and hemiboreal lakes. Our results also demonstrate that a multifaceted approach to the study of phytoplankton compositional and functional change is needed. Freshwater salinization is an increasing environmental threat worldwide that imposes strong physiological stress upon organisms, involving complex responses across multiple levels of biological organization (molecular, organism, population or community level), and which thereby requires the combination of multiple methods to capture them (Cunillera-Montcusí et al., 2022; Fournier et al., 2021). We show that one promising tool is the use of full-time deployed autonomous fluorometers. Optical sensors based on the fluorescence of photosynthetic pigments such as chl-*a* are increasingly being used as a proxy of phytoplankton biomass, as they enable capturing biomass temporal dynamics at a both small and large resolution. Rousso et al. (2021) provide an overview of some of the limitations of these sensors, mainly in relation to differences between day and night fluorescence signals (as also depicted in our measurements), and how to best represent biomass dynamics with that large variation at the daily scale. Rousso et al. (2021) provide useful suggestions for how to correct potential-biased estimates of total phytoplankton biomass based on compensation models and sampling designs though, and our results also show that those day–night fluctuations in fluorescence offer new opportunities to capture responses to environmental stressors. More work is needed to evaluate the tool in a wider range of aquatic systems, including at different depths in deeper systems subjected to pronounced phytoplankton migration patterns and with different dominant phytoplankton species that have different fluorescence signals (Proctor & Roesler, 2010). In addition, a wider range of stressors that affect photosynthesis need to be considered, including, for example, other types of road salt alternatives or additives (Schuler et al., 2017) and increasing temperature (Allakhverdiev et al., 2008), as full-time deployed fluorometers could also aid in understanding and predicting the impact of other stressors on photosynthetic performance. Addressing these open questions will further provide valuable information to plan management practices directed towards avoiding negative effects of salinization and other disturbances on the future ecological status of freshwaters.

CONFLICT OF INTEREST STATEMENT

All authors declare no conflicts of interest.

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SUPPORTING INFORMATION

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