Wetlands as a Local Scale Management Tool to Reduce Algal Growth Potential

Anna Borgström[1] · Lars-Anders Hansson[1] · Johanna Sjöstedt[1]

Abstract

Recent land-use changes have led to a significant loss of natural wetlands worldwide resulting in increased amounts of organic and inorganic compounds reaching lakes and coastal areas. In turn, this has led to an increased algal growth, and subsequently the risk of algal blooms and deteriorated water quality. The capacity of wetlands to retain nutrients is well-known, suggesting that constructed wetlands may be a potential management strategy to mitigate algal blooms in downstream waters, although little is known about seasonal variation in reduction of algal growth potential. Therefore, in a long-term study, we experimentally evaluated the efficiency of seven wetlands to reduce the algal growth potential by comparing the growth in cultures containing 50:50 wetland water from the inlet or outlet and water from a eutrophic lake as a standard inoculum. We show that the majority of the wetlands have a considerable potential to reduce algal growth potential, with up to 89% for cyanobacteria and 73% for green algae. However, there were strong temporal variations in efficiency within, as well as between wetlands. Specifically, we show that the potential to reduce algal growth (standardized conditions) was generally higher in winter than in summer. In addition, the wetlands showed different efficiency in reducing the growth potential of cyanobacteria and green algae. Taken together, our results show that wetlands have a considerable potential to reduce algal growth potential, suggesting that they are an efficient local-scale tool in reducing the risk of algal blooms especially from a future climate change perspective.

Keywords Wetlands · Algal growth · Growth potential · Green algae · Cyanobacteria

Introduction

Global land-use changes caused by rapidly growing human populations have led to a significant loss of natural wetlands, which have been transformed into arable, forested, or urban land (Paludan et al. 2002; Zedler 2003; Hansson et al. 2005). This intensified land use, together with eutrophication, brownification and climate change have led to increasing amounts of organic and inorganic compounds reaching lakes and coastal areas (Ekvall et al. 2013; Wolfe et al. 2013;

Taranu et al. 2015; Kritzberg et al. 2020; Luimstra et al. 2020; Galloway and Cowling 2021).

The import of both organic and inorganic compounds inevitably increases nutrient availability, which is a main factor determining the growth potential of phytoplankton (Anderson et al. 2002; Merel et al. 2013; Beusen et al. 2016; Wurtsbaugh et al. 2019). Consequently, phytoplankton growth has increased in lakes and oceans, often resulting in algal blooms, thus water quality has been reduced worldwide (Heisler et al. 2008; Li and Hong 2011). More specifically, nitrogen (N) and phosphorus (P) are often the limiting nutrients for algal growth and therefore these nutrients are frequently used as key indicators in predicting algal biomass (Tilman et al. 1982; Sterner and Hessen 1994; Dodds 2006; Li and Persson 2018).

In all aquatic systems, phytoplankton are an essential part of the ecosystem, constituting the base of the food web and accounting for almost half of the global primary production (Field et al. 1998; Behrenfeld et al. 2001). Excess algal biomass strongly affects ecosystem services provided by

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lakes, the quality of the raw water and the drinking water production (e.g., by clogging filters, by producing cyanotoxins, causing bad taste and odor, all of which, leads to higher costs due to disinfection) (Willen 2001; Delpla et al. 2009; Merel et al. 2010; Ewerts et al. 2013). Since many bloom-forming phytoplankton taxa, such as cyanobacteria, produce toxins, they are also often harmful to aquatic, as well as terrestrial organisms, including humans (Cronberg et al. 1988; Jonasson et al. 2010; O'Neil et al. 2012; Ekvall et al. 2013; Carmichael and Boyer 2016; Hagman et al. 2019).

Since wetlands are well known to increase the retention of both N and P, they are often used as a tool to improve water quality (Johnston 1991; Mitsch et al. 1995; Zedler 2003; Koskiaho et al. 2003; Vymazal 2007; Cheng et al. 2020). Several ecosystem services are provided by wetlands, such as reducing nutrient concentrations by acting as nutrient traps, retaining sediment, increasing biodiversity, and improving the recreational potential. As a result of the multiple services provided, there is an increasing interest in restoring and constructing wetlands. In turn, this might offer an option to reduce or even reverse the eutrophication process (Mitsch et al. 1995; Koskiaho et al. 2003; Zedler 2003; Hansson et al. 2005; Hoffmann and Baattrup-Pedersen 2007), suggesting that wetland construction may be a potential management strategy to mitigate algal blooms. For example, a recent inventory of wetland efficiency concluded that an increase of only 10% of wetland area may double the N retention at the landscape scale (Cheng et al. 2020), providing incentive for policy decisions regarding wetland restoration and construction. Multiple studies have focused on the nutrient reduction of wetlands, whereas data is still scarce on the potential to reduce algal blooms and especially how this potential varies at the local scale and over time. Here, we evaluated wetlands as a local scale management effort for reducing algal growth potential in a long-term study including seven wetlands.

By retrieving water from the in- and outflows of each wetland and allowing the algae to grow at standardized conditions (20 °C), we aimed to evaluate the potential efficiency of each wetland to reduce algal growth irrespective of temperature constraints, with standardized light and without grazing pressure from zooplankton (here defined as "algal growth potential"). We also aimed to assess the temporal variation in reducing the algal growth potential. As such, the study was performed over 18 months, covering both winter and summer conditions. We hypothesized that the algal growth potential should be lower in the outflow than in the inflow of the wetlands. Hence, in a broader context we expected that wetlands situated upstream of a lake or reservoir should reduce the growth potential of algae and thereby mitigate algal blooms.

Materials and Methods

Seven constructed wetlands with catchment areas of differing sizes and land use (Table 1) were chosen for quantification of the algal growth potential in the water from in- and outflows. The wetlands are located in Kristianstad, Lund and Eslöv municipalities in southern Sweden (Table 1) and were sampled once a month for 18 months, from April 2020 to September 2021. Three liters of water were collected from the inflow and outflow of each wetland, to be used in the experimental set-up. Once a month (in conjunction with the monthly sampling of the wetlands) 10 L of water from Lake Ringsjön was collected, as a standardized algal inoculum. Lake Ringsjön, southern Sweden (55.8642° N, 13.5560° E), is a eutrophic lake with a total phosphorus (TP) concentration of 58 µg L^{-1} and a total nitrogen (TN) concentration of 1 mg L^{-1} (yearly means 2020) (Miljödata-MVM 2021). No additional nutrients were added to the experiment. The collected water from the wetlands and Lake Ringsjön was filtered through a 50 µm mesh to remove grazing zooplankton. Additionally, 40 ml of water was collected in two acid-washed 50 ml centrifuge tubes (Falcon, Corning, USA) for nutrient analysis. TP was measured with the molybdate reactive phosphorus (MRP) method (Menzel and Corwin 1965). TN was measured at the Laboratory of Instrumental

Table 1 Characteristics of the seven wetlands included in the study, including position, year of construction, main land use, area, and maximum depth

Wetland	Coordinates (WGS84)		Constructed (year)	Main catchment	Water area (ha)	Max depth (m)
Viderup	N55.770056°	E13.304722°	2005	Agriculture	2.5	1.1
Fjelkner	N55.967916°	E14.261377°	2018	Agriculture	2.5	1.2
Toarp	N55.948674°	E13.861934°	2017	Forest	1.29	2.0
Lommarp	N56.093608°	E13.854769°	2012	Agriculture	0.75	2.0
Gårdsstånga	N55.768283°	E13.309819°	2002	Agriculture	3	1.5
Venestad	N55.990851°	E13.924788°	2017	Forest	2.4	1.4
Ljungen	N55.937135°	E13.941437°	2017	Agriculture	0.78	1.0

Chemistry managed by the department of Biology, Lund University, using a TOC V-CPH/CPN (Shimadzu) with the method Non-Purgeable Organic Carbon (NPOC).

It should be noted that some wetlands could not be sampled due to drought during summer and early fall, and some were completely frozen during winter. Therefore, no algal growth potential is presented for such sampling dates. The wetlands were also not sampled if the water was stagnant in the in- or outflow of the wetland (i.e. only data from sampling occasion where water was flowing through the wetland were analyzed).

Experimental Set-Up

A culture experiment was set up once a month and run for 14 days to quantify the algal growth potential. Water from the in- or outflow of the wetlands (100 ml 50 μm filtered) were mixed in a 50:50 ratio with Lake Ringsjön water (100 ml, 50 μm filtered), serving as standardized inoculum of algae present in the lake at each sampling occasion. The volume was then adjusted to 160 ml in each culture flask (260 ml Thermo Scientific™ EasyFlask™ (New York, USA)).

There were four replicates for the inflow and outflow, respectively, of the seven wetlands, adding up to a maximum of 56 cultures for each sampling date. The total chlorophyll-*a* and biomasses of cyanobacteria and green algae were assessed in all replicates at day 0 and day 14 of the experiment using an Algae Lab Analyser (ALA, bbe Moldaenke). We focused our analysis on cyanobacteria and green algae since those groups are generally the main problem with respect to toxins (cyanobacteria) and nuisance biomass (green algae and cyanobacteria). In order to mechanistically address the difference in growth potential of algae in the in- and outflow during both summer and winter conditions, the experiment was run in a culture room with a 12 h:12 h light:dark cycle and a constant temperature of 20 °C with an average light intensity of 159 μmol m^{-2} s^{-1}. All replicate culture flasks were lightly agitated and ventilated twice a week. The cultures were placed randomly under the light source and repositioned randomly after ventilation.

Data Analyses

To quantify the change in algal growth potential through each wetland, the difference in algal concentration (total chlorophyll-*a*, cyanobacteria, and green algae) between the in- and outflow was calculated at the end of the experiment (day 14). Specifically, the algal growth potential was calculated by subtracting the algal concentration at day 0 from the concentration at day 14, for the in- and outflow, respectively. At times the subtraction of day 0 led to a negative value for some of the replicates (i.e., the algae did not grow during the 14 days of incubation), the growth was then set to zero.

Thereafter, the change in algal growth potential between the in- and outflow was calculated by subtracting the algal growth potential from the outflow with that from the inflow. Hence, if a wetland is efficient in providing the ecosystem service of reducing the potential for algae to grow, the difference in algal concentration between out- and inflow after 14 days would be negative. All statistical analyses were carried out using GraphPad Prism 9. A two-way analysis of variance (ANOVA) for algal growth potential in each wetland was performed, with multiple comparisons between the in- and outflow for each month. Due to occasional missing values, one wetland (Viderup) was analyzed using a mixed model with multiple comparisons. Greenhouse-Geisser correction was used to assess within-subject effects when an indication that assumptions of sphericity were violated. An un-paired t-test was performed for each wetland, to determine if there was a seasonal difference in the wetland´s ability to reduce TP and TN, respectively.
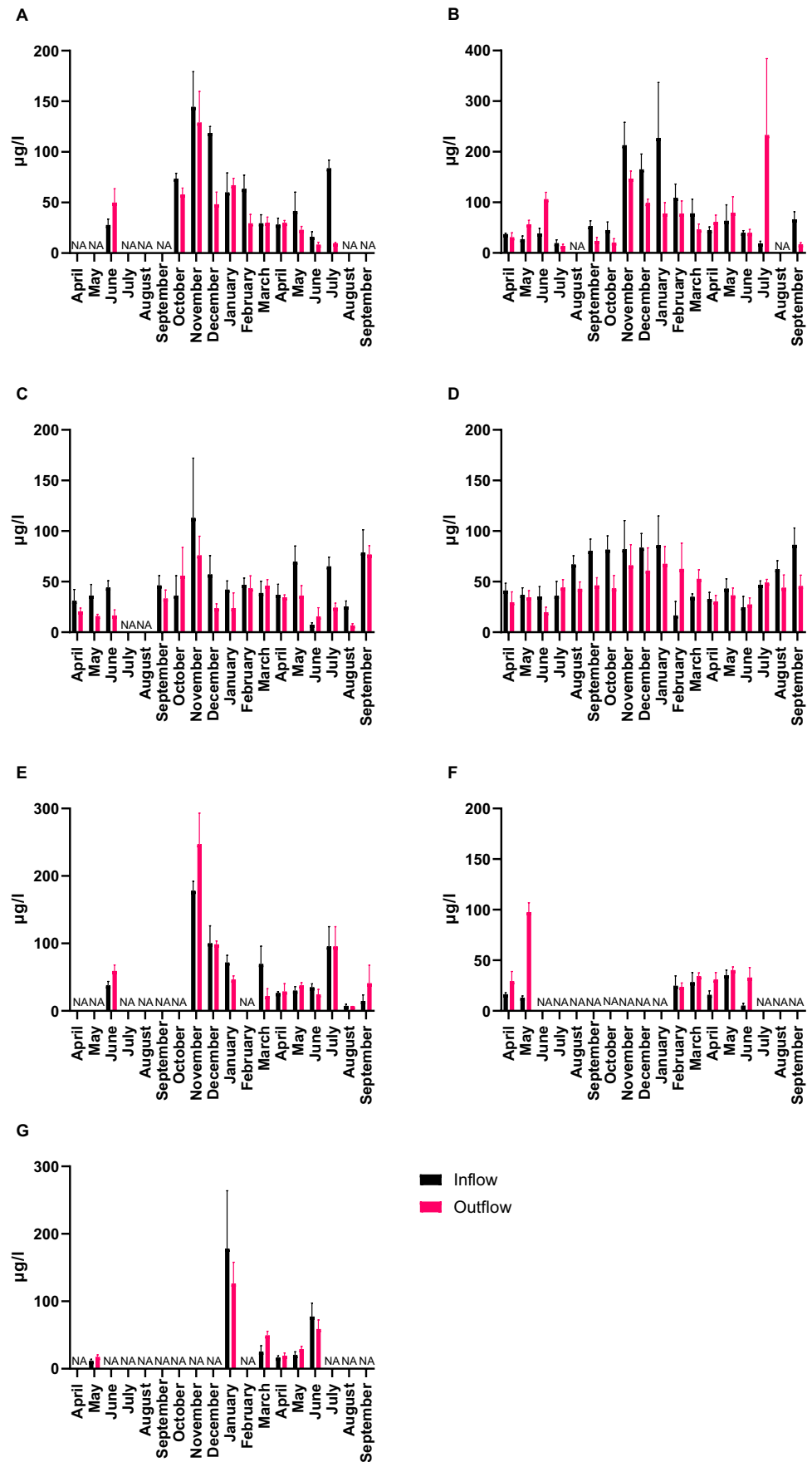
Results

The concentration of total chlorophyll-*a* showed only modest difference between the inflow and outflow of the wetlands at day 0, but the concentration was generally higher in the outflow than in the inflow. At day 14, total chlorophyll-*a* concentrations were generally higher during winter in all wetlands (Fig. 1), even though the phytoplankton biomass was lower at the start of the experiment (day 0; Fig. S1). In four of the wetlands (Fjelkner, Toarp, Lommarp and Viderup) concentrations were generally higher in the inflow. Exceptions from this pattern occurred mainly during spring and early summer (March to June). The concentrations of green algae and cyanobacteria varied seasonally in the wetlands (Fig. S2), as well as in Lake Ringsjön (Fig. S3), generally with higher concentrations during summer than winter. During early spring there was generally an increase in green algae, followed by a decrease during mid to late summer when there was an increase in cyanobacteria instead.

There was a significant effect of location and time for most of the wetlands for total chlorophyll-*a*, green algae, and cyanobacteria (Table 2), indicating that there is a significant difference between in- and outflow, as well as a seasonal variation in reduction of the algal growth potential. However, the interaction between time and location for total chlorophyll-*a*, green algae and cyanobacteria was only significant for the wetland Viderup.

The difference in growth potential of green algae varied considerably after 14 days of incubation, from an increase of 76 μg L^{-1} to a reduction of 113 μg L^{-1} (Fig. 2). However, most wetlands reduced the growth potential of green algae (Fig. 2). Exceptions from this pattern occurred mainly in

Fig. 1 The concentrations of total chlorophyll-*a* (µg/l) in the inflow and outflow of the seven wetlands (*n* = 4), at the end of the experiment (day 14) over 18 months. NA indicates that water was not collected due to drought (summer) or the water being frozen (winter). The seven wetlands are Viderup (**A**), Fjelkner (**B**), Toarp (**C**), Lommarp (**D**), Gårdstånga (**E**), Venestad (**F**) and Ljungen (**G**). Note the difference in scale for B, E and G. The x-axis represents the months of sampling and experimental set-up, starting with April 2020 and ending with September 2021

Table 2 Results for the statistical analyses for growth potential based on total chlorophyll-a, green algae, and cyanobacteria

	Viderup			Fjelkner			Toarp			Lommarp			Gårdsstånga			Venestad			Ljungen		
Total chl	Df	F	P	Df	F	P	Df	F	P	Df	F	P	Df	F	P	Df	F	P	Df	F	P
Location	1, 6	30.530	**<0.01**	1, 6	7.548	**<0.05**	1, 6	21.16	**<0.01**	1, 6	9.806	**<0.05**	1, 6	0.07467	0.794	1, 6	104.4	**<0.001**	1, 6	0.07989	0.787
Time	2.163, 15.54	57.510	**<0.001**	2.495, 14.97	14.28	**<0.001**	2.534, 15.21	13.80	**<0.001**	3.291, 19.75	98.22	**<0.001**	2.648, 15.89	98.22	**<0.001**	3.693, 22.16	19.25	**<0.001**	1.051, 6.307	33.35	**<0.001**
Time x Location	10, 58	9.588	**<0.001**	6, 84	1.171	0.329	6, 84	1.233	0.298	6, 96	1.221	0.302	6, 54	1.592	0.167	6, 36	0.6852	0.663	6, 24	1.245	0.319
Green algae	Df	F	P	Df	F	P	Df	F	P	Df	F	P	Df	F	P	Df	F	P	Df	F	P
Location	1, 6	32.85	**<0.01**	1, 6	3.349	0.117	1, 6	21.97	**<0.01**	1, 6	11.81	**<0.05**	1, 6	0.9420	0.369	1, 6	113.7	**<0.001**	1, 6	2.055	0.202
Time	1.909, 11.07	58.23	**<0.001**	2.169, 13.01	12.74	**<0.001**	2.207, 13.24	13.70	**<0.001**	3.713, 22.28	20.41	**<0.001**	2.189, 13.13	103.9	**<0.001**	3.005, 18.03	15.54	**<0.001**	1.130, 6.777	40.08	**<0.001**
Time x Location	10, 58	10.37	**<0.001**	6, 84	1.244	0.2922	6, 84	0.9134	0.489	6, 96	1.578	0.162	6, 54	1.434	0.219	6, 36	0.9279	0.487	6, 24	1.213	0.334
Cyanobacteria	Df	F	P	Df	F	P	Df	F	P	Df	F	P	Df	F	P	Df	F	P	Df	F	P
Location	1, 6	0.8910	0.382	1, 6	23.13	**<0.001**	1, 6	62.95	**<0.001**	1, 6	4.782	0.071	1, 6	0.3617	0.219	1, 6	2.762	0.148	1, 6	24.44	**<0.01**
Time	1.763, 10.22	8.198	**<0.01**	1.183, 7.099	25.54	**<0.01**	2.095, 12.57	16.85	**<0.01**	3.348, 20.09	65.24	**<0.001**	1.156, 6.935	14.02	**<0.01**	1.1081, 6.489	0.1325	0.747	1.061, 6.365	7.982	**<0.05**
Time x Location	10, 58	37.37	**<0.001**	6, 84	1.968	0.0793	6, 84	0.2939	0.938	6, 96	1.115	0.359	6, 54	1.165	0.339	6, 36	1.042	0.415	6, 24	1.231	0.325

A two-way ANOVA with multiple comparisons were performed for each wetland, except for the wetland Viderup where a mixed model with multiple comparisons was used because of occasional missing values. Location stands for in- and outflow of the wetland and time is over 18 months. Bold text represents significant p-values
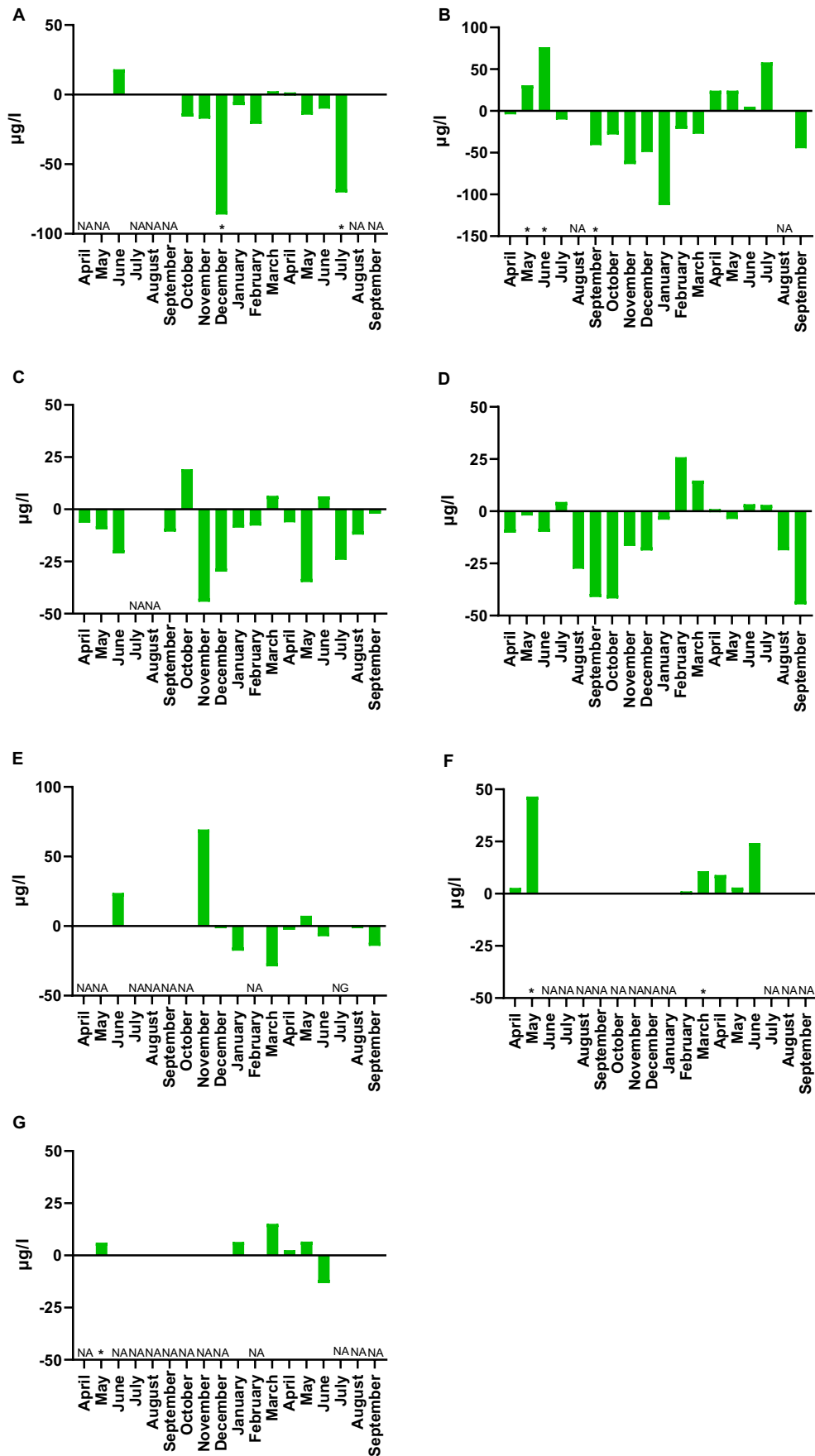
◄**Fig. 2** Growth potential of green algae (difference in biomass, μg/l between out- and inflow at the end of the experiment) for seven wetlands, Viderup (**A**), Fjelkner (**B**), Toarp (**C**), Lommarp (**D**), Gårdstånga (**E**), Venestad (**F**) and Ljungen (**G**). Negative values indicate that the wetland reduced the growth potential. NA indicates that water was not collected due to drought (summer) or the water being frozen (winter). NG denotes no growth of green algae from day 0 to day 14. Significant differences between the in- and outflow are marked with an asterisk. Note the difference in scale for A, B and E. The x-axis represents the months of sampling and experimental set-up, starting with April 2020 and ending with September 2021

spring and early summer (March to June). Some wetlands showed strong fluctuations in efficiency over time (Fig. 2).

Cyanobacteria were mainly present during summer and fall and the differences in growth potential of cyanobacteria between out- and inflow were far lower than for green algae, ranging between an increase of 0.9 μg L^{-1} and a reduction of 3.1 μg L^{-1} (Fig. 3). Most wetlands varied considerably over time in their efficiency to reduce cyanobacterial growth potential, but Fjelkner, Lommarp, Venestad and Ljungen reduced the growth potential of cyanobacteria for most sampling time points (Fig. 3).

There was an overall reduction in green algae growth potential over the 18 months, except for Gårdstånga, Venestad and Ljungen (Fig. 4), which had an overall increase in algal growth potential. There was generally a reduction in the growth potential of total chlorophyll-*a* for the wetlands, with only two wetlands showing an increase in growth potential (Gårdstånga & Venestad; Fig. 4). The overall growth potential for cyanobacteria was reduced in all wetlands except for Gårdstånga (Fig. 4).

In addition to showing that the wetlands generally, and especially during winter, reduced the overall chlorophyll level, our analysis of algal growth potential shows that wetlands differed in their efficiency in reducing different algal taxa. For example, Viderup reduced green algae, but was less efficient at reducing cyanobacteria, whereas Venestad was generally efficient in reducing the growth potential of cyanobacteria, but not green algae.

The wetlands retained nutrients equally efficient irrespective of season (April to September versus October to March, un-paired t-test > 0.05 for all wetlands, Figs. S4 and S5). Generally, the wetlands were P limited during winter and spring and N limited during summer and autumn, except for Lommarp, which was generally limited by P throughout the study period (Table 3).

Discussion

During recent decades, the restoration of old wetlands and construction of new ones has become a common tool in managing and counteracting nutrient-rich runoff (Cheng et al. 2020). By decreasing nutrient levels in the water,

wetlands may also reduce algal growth. However, little is known about the temporal and spatial variations in the efficiency of wetlands to reduce algal growth potential and how to optimize their function to counteract algal blooms in lakes and oceans. Our results clearly show that constructed wetlands situated upstream of a lake or ocean can reduce algal growth potential and thereby mitigate algal blooms downstream (Fig. 4).

The efficiency in reducing algal growth potential of green algae among wetlands differed considerably. However, 61% of the monitored wetlands reduced algal growth potential in more than 63% of sampling occasions. Only two wetlands (29%, Ljungen and Venestad) were inefficient most of the time and rarely reduced green algal growth potential. Although the wetland Gårdstånga generally reduced the growth potential of total chlorophyll-*a* and green algae (Fig. 2), the overall effect during 18-month sampling period was instead an increase in growth potential (Fig. 4). Most wetlands (86%) reduced the growth potential of cyanobacteria, at least 50% of the time. Only one wetland (Viderup) was irregular in its reduction of growth potential of cyanobacteria, although the overall effect was a reduction in growth potential (Fig. 4). Only one wetland (Gårdstånga) had an overall increase in growth potential of cyanobacteria. These results suggest that most wetlands are efficient in reducing the risk of algal blooms irrespective of season. Overall, the growth of cyanobacteria during the experiments was low, which could be due to that they were outcompeted by faster growing green algae that were released from grazing pressure by zooplankton during the experiments. It should also be noted that in our experimental set-up, where temperature and grazer effects were standardized, the wetlands were more efficient in reducing algal growth potential during winter.

In addition, our results showed that wetlands differ in their efficiency in reducing the growth potential of different algal taxa. For example, Viderup reduced green algae, but rarely cyanobacteria, whereas Venestad was generally efficient in reducing growth potential of cyanobacteria, but not green algae. The reasons for these differences are unknown but indeed deserve future research. There were also temporal variations in the efficiency of reducing different algal taxa, where the growth potential of cyanobacteria increased, whereas it decreased for green algae and vice versa (for example July and September 2021 for Fjelkner Figs. 2 and 3). The difference in wetland efficiency when it comes to reducing different algal taxa could be connected to the nutrient concentrations, since N and P often limit phytoplankton growth and abundance, as well as affect phytoplankton community composition (Tilman et al. 1982; Sterner and Hessen 1994; Dodds 2006; Bergström 2010; Li and Persson 2018).

In systems where N is the limiting resource for phytoplankton growth, N-fixing cyanobacteria can increase since
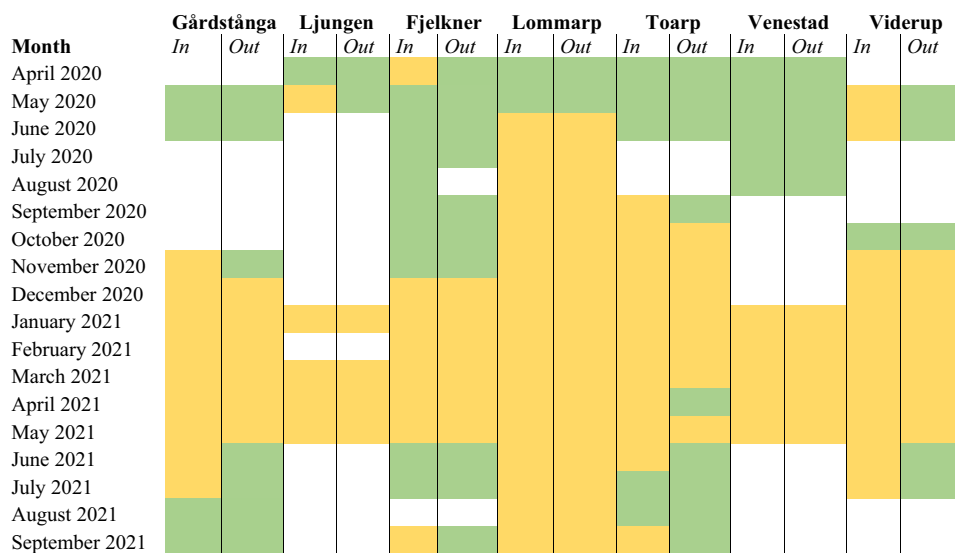
Fig. 3 Growth potential of cyanobacteria (difference in biomass, µg/l between out- and inflow at the end of the experiment) for the seven wetlands, Viderup (**A**), Fjelkner (**B**), Toarp (**C**), Lommarp (**D**), Gårdstånga (**E**), Venestad (**F**) and Ljungen (**G**). Negative values show that the wetland reduces the growth potential. NA indicates that water was not collected due to drought (summer) or the water being frozen (winter). NG denotes no growth of cyanobacteria from day 0 to day 14 whilst NC denotes no cyanobacteria present for that month. Significant differences between the in- and outflow are marked with an asterisk. Note the difference in scale for A, B and D. The x-axis represents the months of sampling and experimental set-up, starting with April 2020 and ending with September 2021
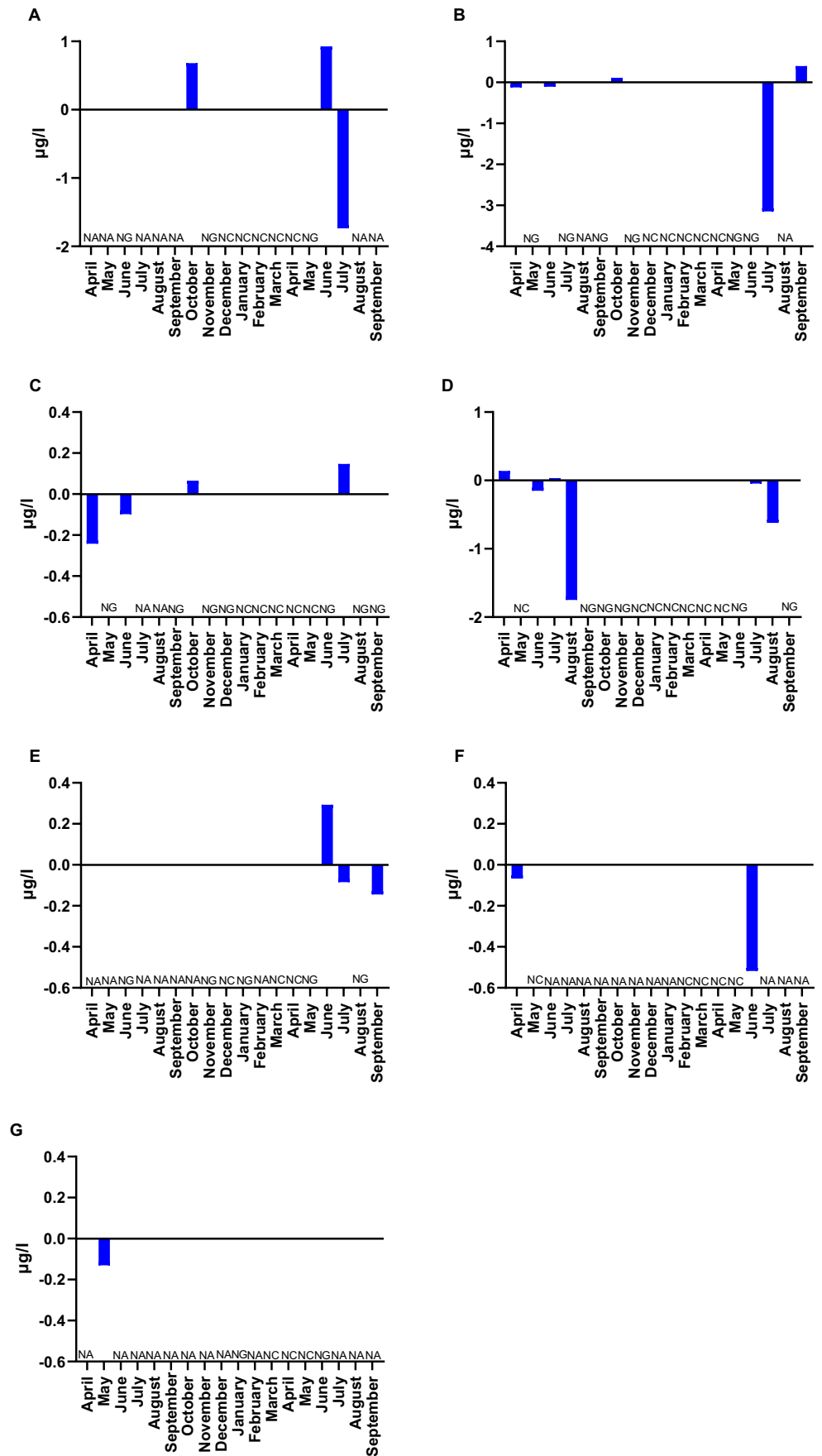
Fig. 4 Average difference in (**A**) total chlorophyll-*a* (µg/l) and green algae (µg/l), respectively; and (**B**) cyanobacteria (µg/l) between the inflow and outflow during the 18-month sampling period, for the seven wetlands. Generally, the wetlands reduced the growth potential both assessed as total chlorophyll-*a*, green algae, and cyanobacteria. Exceptions are the wetlands Ljungen, Gårdstånga and Venestad regarding total chlorophyll-*a* and green algae. Only Gårdstånga increased the algae growth potential for total chlorophyll-*a*, green algae, and cyanobacteria. Cyanobacteria is presented in a separate graph due to lower abundances compared to green algae
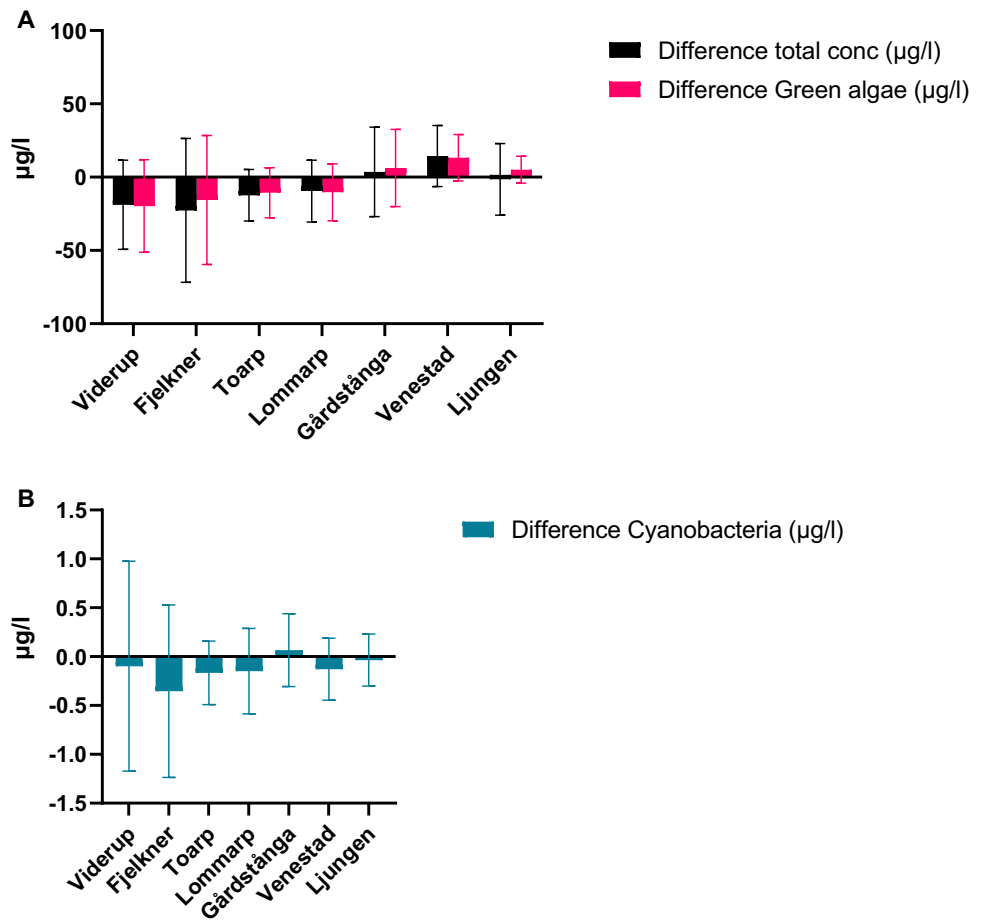
Table 3 To visualise if the wetlands were limited by nitrogen (N) or phosphorus (P) over the 18-month sampling period, shown with colors indicating if the N:P ratio is above (P-limited, shown in yellow) or below (N-limited, shown in green) 16:1

Month	Gårdstånga In	Gårdstånga Out	Ljungen In	Ljungen Out	Fjelkner In	Fjelkner Out	Lommarp In	Lommarp Out	Toarp In	Toarp Out	Venestad In	Venestad Out	Viderup In	Viderup Out
April 2020														
May 2020														
June 2020														
July 2020														
August 2020														
September 2020														
October 2020														
November 2020														
December 2020														
January 2021														
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July 2021														
August 2021														
September 2021														

The wetlands were generally P-limited during winter and spring and N-limited during summer and autumn. Boxes without a color indicate that water could not be collected because the wetlands were dry during summer or completely frozen during winter

they utilize N from the atmosphere and then take advantage of the excess P (Schindler et al. 2008). Hence, for cyanobacteria, P may set the capacity for growth and abundance in most wetlands (Schindler et al. 2008; Carvalho et al. 2013; Li and Persson 2018), whereas a few studies have shown that green algae are generally limited by N (Yeesang and Cheirsilp 2011; Smith and Lee 2012). When there is a high N:P ratio, that is a P limitation, in the wetlands during winter and spring (Table 3), there were generally no cyanobacteria present. Instead, cyanobacteria were present during summer and autumn when the N:P ratio generally was low. The N:P ratio did not seem to affect the presence of green algae in the wetlands. However, the highest reduction in growth potential for green algae was generally reached during winter (Fig. 2), when the N:P ratio in the wetlands were generally high, thus there was a higher concentration of N in relation to P. However, our study was not designed for a more detailed analysis of the effects from stoichiometric variations.

The observation that some of our constructed wetlands dried up during summer is of considerable importance given the ongoing climate warming, likely leading to enhanced levels of evaporation and more frequently dried-out wetlands. The seasonal variation in temperature generally affects nutrient uptake and release rates of nutrients in wetlands. Constructed wetlands have been shown to have maximum efficiency for nitrate removal during summer (Spieles and Mitsch 2000), which is a result of higher rates of microbial activity and macrophyte growth during the growing season (spring and summer) (Scholz and Lee 2005; Yang et al. 2016; Nilsson et al. 2020). On the contrary, our results, performed at standardized conditions with respect to light and temperature, showed that the wetlands are more efficient in reducing algal growth potential during winter than summer. Despite the wetlands being more efficient during winter (removing temperature restrictions), there were no significant difference in reduction of nutrient concentrations between winter and summer in the wetlands (Figs. S4 and S5). Hence, wetlands seem to be able to efficiently reduce nutrient concentrations even in winter, although the phytoplankton biomasses were low (Fig. S1). Moreover, low phytoplankton biomass in the wetlands during winter, and thereby clearer water, may have improved the light penetration, allowing periphytic algae at the bottom to grow (Hansson 1988; Hansson 1992; Vadeboncoeur et al. 2014). Hence, a possible mechanistic explanation for high nutrient retention in winter may be that an increase in periphytic algae bind nutrients in the wetlands, leading to a reduction in nutrient concentrations. However, it is beyond the scope of our study to evaluate the periphyton growth and its influence on the ability of wetlands to affect nutrient retention. The implications of this mechanistic finding are mainly that in a future climate warming situation, there is a considerable potential of constructed wetlands to be even more useful

as tools to counteract the increasing risk of algal blooms in lakes and oceans.

The reduction of nutrients by wetlands (Johnston 1991; Koskiaho et al. 2003; Zedler 2003; Vymazal 2007; Cheng et al. 2020) is potentially the main factor determining algal growth. This is supported by our results, as the majority of the wetlands had the capability to reduce algal growth potential. However, there were temporal fluctuations within, as well as among wetlands. Despite the strong fluctuations, there was a pattern showing that some wetlands can reduce the algal growth potential between in- and outflow with up to 89% for cyanobacteria and 73% for green algae, whereas a minority of the wetlands were inefficient, and even increased the growth potential between in- and outflow. Based on this we conclude that wetlands are generally efficient as a local scale management tool to reduce nutrient concentrations and algal growth potential even in winter, which in a climate change context of prolonged growth seasons and warmer temperatures may be of importance. Hence, if the water from a catchment passes through a wetland situated upstream of a lake, the algal growth potential in the lake is in most cases significantly reduced. From a broader perspective this is of considerable importance for the water quality and the ecosystem services provided by downstream lakes, rivers, and coastal areas, indeed providing management incentives for restoring and constructing wetlands in the landscape.

Declarations

Competing Interests The authors have no financial interests.

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