Macrophyte removal affects nutrient uptake and metabolism in lowland streams

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A B S T R A C T

Macrophytes provide essential ecosystem services in lowland streams, including nutrient uptake that can reduce downstream transport to vulnerable coastal areas. Despite that, to ensure water conveyance and effective run off from agricultural fields, aquatic plant biomass is removed regularly in many European streams (i.e. weed cutting practices). However, the impacts of weed cutting on stream ecosystem processes are not yet well documented. Here, we studied the effect of weed cutting on nutrient retention and ecosystem metabolism in three lowland streams with contrasting dominant vegetation communities (submergent and emergent plants) during summer in Denmark. Our results showed a decrease in nutrient retention; uptake velocity of ammonium decreased 34–77 % and of phosphate decreased 50–77 %. Ecosystem metabolic rates also decreased after weed cutting, both in gross primary production (9 %, 60 % and 85 %) and respiration (47 %, 69 % and 76 %). The effects of weed cutting on these ecosystem processes prevailed three weeks after the cutting occurred. Understanding the effects of weed cutting on stream ecosystem functioning can improve nature-based management strategies to control eutrophication of downstream coastal areas.

1. Introduction

Macrophytes are considered ecosystem engineers because they play an essential ecological role in shallow aquatic ecosystems by modifying the physical and chemical environment (e.g. Carpenter and Lodge, 1986; Jones et al., 1994). They also provide essential ecosystem services, which include habitat and food provision (e.g. for invertebrates and fish) and regulation of ecosystem processes, such as nutrient cycling (Preiner et al., 2020; Riis et al., 2020a; Thomaz, 2021). For example, Levi et al. (2015) showed that macrophytes and their associated epiphytic biofilms accounted for 71–98 % of the ammonium uptake at reach scale, and Riis et al. (2012) showed that macrophyte habitats had four times higher ammonium uptake rates than non-macrophyte habitats in lowland streams. Similarly, Balestrini et al. (2018) found that uptake velocity was 9.8-fold for ammonium and 4.4-fold for phosphate faster in a macrophyte rich reach compared to an unvegetated reach.

Macrophyte mediated nutrient uptake is driven by several mechanisms besides direct uptake by leaves and roots (Riis et al., 2020b). First,

macrophyte beds increase water-biota contact time due to increased water residence time within the beds allowing for longer periods of nutrient uptake. Second, macrophyte beds promote deposition of fine particulate matter, which can stimulate recycling of organic matter and associated nutrients by invertebrate and microbial communities (Clarke, 2002). Third, macrophytes can enhance nitrogen removal by denitrification due to high organic matter contents and anoxic conditions promoted by fine particulate organic matter deposition associated with macrophyte beds (Audet et al., 2021).

Macrophytes show a variety of growth forms that reflect adaptations to their physical habitat, which in turn can control the effect of the plants on ecosystem processing (Pan et al., 2023). They can be classified into two growth forms, submerged and emergent plants (Bowden et al., 2017). Submerged plants dominate the permanent wetted area of the stream profile, acquire nutrients and inorganic carbon from the water and sediment (Madsen and Cedergreen, 2002; Balestrini et al., 2018). Emergent plants are most frequent along stream margins and have aerial photosynthetic parts, acquiring nutrients from the sediment and carbon

dioxide from the atmosphere (Bowden et al., 2017). Occasionally, emergent plants can occupy the whole stream profile in small slow-flowing streams, leaving limited space for autotrophic production within the stream because of high light interception, whereas in faster flowing streams, submerged plants will likely dominate (Riis et al., 2001).

Macrophyte removal (i.e. weed cutting) is a common management practice in many European streams and other parts of the world (e.g. New Zealand) to ensure water conveyance and avoid flooding over the agricultural fields (Hussner et al., 2017; Thiemer et al., 2021). Mechanical removal of aquatic macrophytes can be conducted either manually (e.g. by using a scythe) or by using heavy machinery for example with a boat mounted with automatic knives, which can target macrophytes cutting above the sediment or to be forced into the sediment (e.g. Rasmussen et al., 2021). The nature and timing of weed cutting is dependent on the regional guidelines, technical constraints, stakeholder motivations and legal requirements. In Denmark, for example, 80 % of midsized streams receive weed cutting typically from April to November and the weed cutting frequency has increased from 1 to 2 cutting a year to 2–3 cuttings (or even higher) during the last decades (Baattrup-Pedersen et al., 2018). Weed cutting has immediate and severe consequences for in-stream habitat by increasing water velocity and transported suspended sediment (Clarke, 2002; Levi et al., 2015; Sand-Jensen, 1998) and recently it was also associated with an overall decrease in system diversity (Misteli et al., 2023). On a longer term, frequent weed cutting can also reduce macrophyte species diversity and homogenize community composition (Baattrup-Pedersen et al., 2003, 2002) and streams that are regularly cut often fail to fulfill ecological goals (Baattrup-Pedersen et al., 2018). Whereas it is well established that weed cutting significantly affects the physical and biological structure of streams, effects of cutting on stream ecosystem functions including nutrient cycling and metabolism are not yet well documented (Thiemer et al., 2021), and the effects might even depend on the dominant plant types in the macrophyte community (i.e. floating, emergent and submergent because studies have shown that e.g. primary production and nutrient uptake vary across freshwater plant types (e.g. Manolaki et al., 2020; Sand-Jensen et al., 2022).

In the present study, we examined how weed cutting affects inorganic nutrient uptake and metabolism in three agricultural lowland streams. We hypothesized that macrophyte removal will cause a significant impact to stream nutrient uptake and metabolic rates, i.e. gross primary production (GPP) and ecosystem respiration (ER), and these effects will vary depending on the dominant plant community. In streams dominated by submerged vegetation, we expected that macrophyte removal will cause a significant decrease in both nutrient uptake and metabolic rates, reflecting the assimilatory demand of plants and associated biofilms. We also expected a decline of nutrient uptake in streams dominated by emergent plants due to reduced biofilm habitat, but metabolic rates may be affected differently; whereas GPP may be stimulated with the increase of benthic zone light availability and autochthonous carbon fixation, ER may decrease due to the decrease of autotrophic and heterotrophic (e.g. microbes colonizing macrophytes) respiration. We expected limited ecosystem functioning recovery over the experimental time period of three weeks.

2. Materials and methods

2.1. Study design and sampling sites

To study the effect of a weed cutting event, we used a full before–-after-control–impact (BACI) design with an impacted reach (i.e. 'impact') experiencing weed cutting and a control reach (i.e.'control') without weed cutting (Underwood, 1991). In all streams, the control reach was placed upstream of the impacted reach to account (i.e. ca. 500–700 m) for effects of changes in temperature and light between the sampling campaigns. We measured three agricultural lowland streams

near Aarhus, Jutland, Denmark (Fig. 1): Aarhus (56°04'28.4"N 10°05'11.3"E), Lille (56°14' 59.6"N, 10°03'57.1"E), and Vadsted (56°15'02.0"N 9°50'03.3"E). Aarhus, Lille and Vadsted are open-canopy streams with a relatively channelized course. In Vadsted, a wastewater treatment plant is located upstream of the study site, resulting in increased ammonium concentrations in this stream. Nitrate concentrations are highest in Lille stream (Table 1). The impacted reach in Vadsted has an inlet from a lake and surrounded areas were devoted to pastoral land use. At each sampling time, stream water conductivity was measured at the upstream and downstream stations using WTW - Portable conductivity meter ProfiLine Cond 3310 as an indicator of potential groundwater inputs. The percentages of change for all the cases were small (<2 %), indicating no significant inputs along the reaches (Table A1).

The macrophyte biomass was cut with a scythe at maximum biomass (July-August) following regional regulations. In Aarhus and Lille, vegetation was reduced by 74 % and 83 %, respectively, with the highest intensity confined to the central parts of the stream channel, and by 99 % in Vadsted (Table 1).

The study was conducted during a five-week period in Aarhus and Lille in 2018 (June to July,) and in Vadsted in 2020 (August to September) and included three discrete sample dates: one week prior to the weed cutting (i.e. 'Before'), one week after cutting (i.e. 'Wk1'), and three weeks after weed cutting (i.e. 'Wk3'). The selected reaches were selected to be representative of the stream, without major lateral inputs of water, with a length of 118–270 m. We acknowledge that sampling the study streams over two separate years may not be ideal but it was necessary due to differences in weather conditions (Fig. A1) but was due to logistic constraints. However, by applying the BACI design to compare control and impact reaches within the study period any year-to-year variation should not cause any major impact on the effect of weed cutting.

Aarhus and Lille were dominated by submergent macrophytes (*Potamogeton crispus* and *Ranunculus aquatica*, respectively). Vadsted was dominated by the emergent macrophyte *Iris pseudacorus* in the impacted reach, whereas submergent macrophytes (*Potamogeton natans* and *Callitriche* sp.) dominated in the control reach. In Vadsted, sediment at the control site consisted of almost equal parts of stone (> 2 cm), gravel (2 mm-2 cm), and sand (< 2 mm), while the impact site was dominated by stone and sand, with a minor amount of gravel. Both the control and the impact site in Aarhus consisted of equal parts of stone, gravel and sand, while both sites in Lille were dominated by gravel and sand, with a minor amount of stone.

2.2. Physicochemical and biological parameters

During all sampling periods, we quantified the physical, chemical, and biological characteristics of the stream reaches. For each sampling, three water samples were collected upstream and downstream of each reach, transported on ice to the laboratory, filtered through pre-muffled Whatman GF/F filters and stored frozen until analysis. Samples were analyzed for ammonium (NH_4^+), nitrate (NO_3^-) and orthophosphate (PO_4^{3-}) using a Lachat QC-8500 Flow Injection Autoanalyzer (Lachat Instruments, Loveland, Colorado, USA). In Vadsted, we recorded turbidity at 10- min interval at the downstream station of the impact reach using an EXO 3 Sonde (YSI, Yellow Springs, Ohio).

For every sampling and reach, we measured width and depth of 7–17 transects and quantified the macrophyte cover (3 types: submergent, emergent and filamentous algae) and substrate cover (4 types: stone, gravel, sand, and mud). The macrophyte cover was estimated as percentage of the total width. For each transect, we further calculated the volume of the macrophytes (either submergent, emergent or filamentous algae) as the percentage of macrophyte cover multiplied by the transect area (width (w, in m) and length (1 m)) and the height of the macrophytes (h, in m):
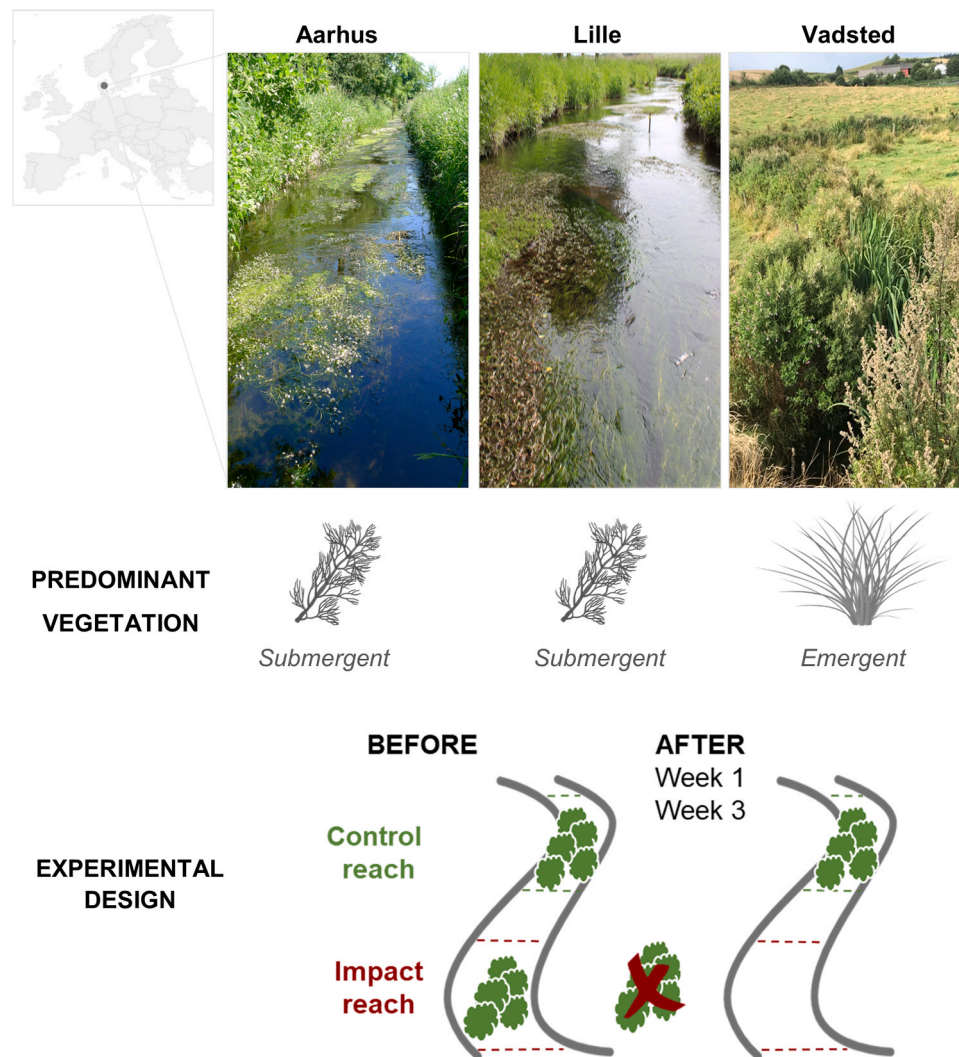
Fig. 1. Sampled streams and study design. Source of plant symbols: Integration and Application Network (ian.umces.edu/media-library).

$$V_{macrophyte} = Macrophyte \quad cover * (w \bullet l \bullet h \quad)$$

The macrophyte volume was averaged for all transects to provide average macrophyte biomass volume per stream length (m^3 of macrophyte m^{-2} stream reach (Bowden et al., 2017).

We determined chlorophyll a (chl a) of biofilm on sediment (episammon) and on stones (epilithon) from samples previously frozen (4 replicates each) in Aarhus and Lille, by extracting them with ethanol (95 %) in dark for 18–24 h, centrifuging, and analyzing the chl a extract at a UV spectrophotometer (Shimadzu). In 2020, we simplified the method for Vadsted sampling, and we measured chl a per substrate area using BenthoTorch ™ (bbe Moldaenke, Germany) (i.e. 9 measures per reach and substrate). As such, we cautiously used chl a data to relatively compare between control and impact reaches within the same stream, but not among streams. We estimated the habitat weighted chl a (in μg cm^{-2}) considering the percentages of the predominant substrate in each reach (i.e. gravel and sand) as following:

$$Habitat \; weighted \; Chl \; a = \frac{(Chla_{Epilithon} \bullet \%gravel) + (Chla_{Episammon} \bullet \%sand)}{100}$$

2.3. Pulse nutrient addition experiments and hydraulics

We determined NH$_4^+$ and PO$_4^3$ uptake rates at each stream reach and at each sampling time (i.e. before, Wk1 and Wk3) using pulse addition techniques (Álvarez et al., 2010; Martí and Sabater, 2009). A carboy containing 5 L of stream water, 1 kg of sodium chloride and reach-specific nutrient amounts (KH$_2$PO$_4$ and NH$_4$Cl) was released in a single pulse at the head of each reach, where appropriate mixing was ensured. We calculated the specific amounts of nutrients by considering the discharge and basal concentrations from the previous sampling at the reach with the objective to achieve a maximum tenfold increase in N and P concentrations at the peak of the slug event. Nevertheless, the measured concentrations observed at the peak of the slug event exhibited variability, as indicated in Table A2. Despite the short duration of the elevated nutrient levels during the release, they may have saturated the demand (Tank et al., 2008). However, it remains challenging to determine this without conducting multiple releases at various concentrations and measuring the corresponding effects.

Conductivity changes were continuously recorded at the downstream station and collected water samples were collected at different time intervals during the breakthrough curve (~ 30 water samples per release in total). For the nutrient uptake measurements, we selected an experimental subreach at each studied reach, which varied from 80 to 183 m length with travel times from 7 to 17 min.

Water samples obtained during the pulse addition were filtered in the field using pre-muffled Whatman GF/F filter and analyzed for NH$_4^+$ and PO$_4^{3-}$ concentrations using a Lachat Autoanalyzer, as previously described. In Lille, we had to discard the pulse addition-experiment due to initial high background solute concentrations, which hampered us to correctly assess solute added in this stream at the "before" sampling

Table 1

Biological and physiochemical properties of the sampled streams reaches before and one ('Wk1') and three ('Wk3') weeks after the weed cutting. The variables included are discharge (Q, L s^{-1}), and mean velocity (min), mean water nutrient concentration (mg L^{-1}, n = 6), mean water temperature (Temp., °C, n = 2016 except before measurements in Vadsted, n = 506), dissolved oxygen concentrations (DO, mg L^{-1}, n = 506), macrophyte abundance (m^3 m^{-2}) of submergent (Sub.) and emergent (Em.) macrophytes and filamentous algae (Fil.), and habitat corrected chlorophyll a (µg cm^{-2}); na stands for non-available data and SE stands for standard error.

Stream reach	Sampling time	Q L s^{-1}	Mean velocity m s^{-1}	Nutrient concentration mg L^{-1} (SE)			Temp ° C (SE)	DO mg L^{-1} (SE)	Volume macrophyte/stream reach (m^3 m^{-2})			Chl a µg cm^{-2}
				NH$_4^+$	NO$_3^-$	PO$_4^{3-}$			Sub.	Em.	Fil.	
Aarhus												
Control	Before	50.6	0.21	0.03 (0.002)	0.23 (0.02)	0.04 (0.002)	18.1 (0.06)	7.9 (1.1)	0.086	0.004	0.022	5.62
	Wk1	21.7	0.10	0.03 (0.002)	0.12 (0.01)	0.04 (0.002)	19.2 (0.06)	6.7 (1.1)	0.111	0.002	0.029	8.78
	Wk3	17.8	0.10	0.06 (0.018)	0.26 (0.01)	0.08 (0.003)	20.0 (0.06)	7.0 (1.1)	0.094	0.007	0.020	9.73
Impact	Before	52	0.13	0.03 (0.001)	0.23 (0.02)	0.04 (0.001)	17.9 (0.07)	7.6 (1.5)	0.359	0.078	0.016	8.18
	Wk1	22.5	0.12	0.03 (0.002)	0.13 (0.01)	0.05 (0.002)	19.2 (0.07)	7.5 (1.4)	0.103	0.012	0.001	7.38
	Wk3	17.9	0.10	0.04 (0.002)	0.26 (0.01)	0.08 (0.003)	20.0 (0.06)	7.4 (1.4)	0.104	0.014	0.010	7.48
Lille												
Control	Before	57.8	0.16	0.08 (0.005)	1.85 (0.09)	0.02 (0.001)	12.6 (0.04)	8.1 (0.3)	0.064	0.027	0.000	3.83
	Wk1	46.4	0.14	0.04 (0.002)	1.45 (0.17)	0.02 (0.002)	13.2 (0.05)	8.3 (0.3)	0.046	0.021	0.001	1.56
	Wk3	42.9	0.13	0.04 (0.002)	1.37 (0.11)	0.02 (0.001)	na	na	0.049	0.012	0.001	3.60
Impact	Before	96.5	0.15	0.07 (0.004)	1.39 (0.13)	0.02 (0.001)	12.6 (0.04)	8.1 (0.3)	0.324	0.047	0.000	4.25
	Wk1	84	0.18	0.04 (0.002)	1.57 (0.11)	0.03 (0.002)	13.2 (0.05)	8.3 (0.3)	0.064	0.000	0.000	4.18
	Wk3	80.6	0.27	0.04 (0.002)	1.51 (0.12)	0.02 (0.001)	na	na	0.037	0.011	0.003	4.17
Vadsted												
Control	Before	16.5	0.32	0.25 (0.006)	0.62 (0.01)	0.07 (0.002)	17.2 (0.05)	3.9 (0.7)	0.007	0.002	0.002	1.17
	Wk1	10.8	0.23	0.32 (0.008)	0.77 (0.01)	0.07 (0.003)	15.8 (0.02)	4.0 (0.3)	0.006	0.004	0.001	0.61
	Wk3	6.5	0.17	0.17 (0.008)	0.96 (0.06)	0.05 (0.003)	14.9 (0.04)	3.9 (0.4)	0.008	0.002	0.003	0.35
Impact	Before	29.5	0.15	0.21 (0.008)	0.65 (0.01)	0.07 (0.004)	17.7 (0.06)	8.8 (1.1)	0.061	1.781	0.000	na
	Wk1	9.4	0.24	0.14 (0.008)	0.70 (0.02)	0.05 (0.003)	15.3 (0.12)	9.6 (0.7)	0.002	0.020	0.000	0.05
	Wk3	6.8	0.21	0.10 (0.006)	0.71 (0.01)	0.06 (0.002)	14.8 (0.05)	9.4 (0.4)	0.002	0.024	0.000	0.05

time.

Discharge was estimated with the salt-release method (Gordon, 2004), and mean water velocity (m s^{-1}) was calculated as the reach length divided by the time half of the added salt used traveling to the downstream station.

We used a mass-balance approach to calculate three gross nutrient uptake metrics for each nutrient pulse addition (Martí and Sabater, 2009): the uptake rate coefficient (Kt, s^{-1}), the uptake velocity (v_f, mm min^{-1}) and the areal uptake rate (U, µg m^{-2} min^{-1}).

$$K_t = \frac{\ln\left(\frac{M_a}{M_r}\right)}{t}$$

$$v_f = \frac{\left(\frac{Q}{a}\right)}{\frac{v}{K_t}}$$

$$U = C * v_f$$

where t is the time (in seconds) required to return to background concentrations, M_a is the added solute mass (g), and M_r is the recovered solute mass (g), v is water velocity (m s^{-1}), Q is discharge (m^3 s^{-1}), a is average channel width (m), C is the added solute (i.e. NH$_4^+$ or PO$_4^{3-}$) background concentration. We acknowledge that the comparison of these estimates with the well-established literature data should be

considered with a degree of caution since pulse addition generally result in lower uptake rates than constant rate additions (Álvarez et al., 2010).

We calculated uptake-to-export ratios (i.e. UE ratio) to estimate the nutrient export compared to nutrient uptake in a 500 m fixed stream reach (Myrstener, 2020):

$$UE \quad ratio = \frac{U * w * 500}{Q * [C]}$$

where U is the areal uptake (mg m^{-2} s^{-1}), w is the stream width (m), Q is the discharge (in L s^{-1}), and C is the solute (NH$_4^+$ or PO$_4^{3-}$) concentration (mg L^{-1}). Ratios above 1 indicate that solute uptake is higher than export.

To visualize changes on uptake velocity (v_f), areal uptake (U) and UE between a time and the previous time, we used log10-transformed response ratios R ratio, calculated as Log$_{10}$ (R$_{Wk1}$ = Wk1/Before) and Log$_{10}$ (R$_{Wk3}$ = Wk3/Wk1) (Levi and McIntyre, 2020). We interpreted that weed cutting might have had an ecological impact to the stream functionality, when |R$_{impact\ reach}$| > than |R$_{control\ reach}$|. We interpreted a recover of stream functions at the impact reach when R$_{Wk3}$ > 0, and, and when R$_{wk3}$ in the impact reach was higher than R$_{wk3}$ in the control reach.

2.4. Stream metabolism

We measured dissolved oxygen (DO) concentrations, water temperature and light at 5 min intervals to estimate metabolism. We installed miniDOT oxygen loggers (Precision Measurement Engineering Inc.) at the upstream and downstream stations of every stream reach. The average travel times were 23 min in Aarhus, 30 min in Lille, and 13 min in Vadsted. We acknowledge that these reaches are generally shorter than recommended (>0.4 v/k; Reichert et al., 2009) and highly affected by the top station. However, the research selection was constrained by lateral water inputs (e.g. drainage pipes, adjacent lake inflow and outflow) and it was not possible to select longer reaches. MiniDOT loggers were intercalibrated to 100 % O_2 saturation in bubbling water for Aarhus and Lille, and to a new factory-calibrated miniDOT for Vadsted. We installed HOBO Pendant Temperature/Light loggers (model UA-002–64, Onset Computer Corporation) to record light intensity (in Lux) above water level (in the case of Vadsted, the logger was cover by the tall emergent vegetation). In Vadsted, we also deployed Odyssey PAR loggers (Dataflow Systems Ltd.) that recorded photosynthetically active radiation (PAR). We then established a Lux-PAR polynomic relationship to convert HOBO readings to photosynthetic photon flux density (PPFD, µmols photons m^{-2} day^1).

Reach-scale metabolism and reaeration parameters were estimated by fitting two-station metabolism models to observed DO data. In a general form, the model can be described as:

$$DO_{dw,t+\Delta t} = DO_{up,t} + GPP - ER + Gas \quad exchange$$

where DO concentration (g m^{-3}) at a downstream station and time t plus travel time Δt is equal to DO at an upstream station at time t and allowing for O_2 production and consumption fluxes along the reach: gross primary production (GPP), ecosystem respiration (ER) and air-water O_2 exchange. In its specific form, the model can present some variants depending on the expected influence of light and temperature on GPP, ER and reaeration (Hall et al., 2016; Song et al., 2016). We chose the following model formulation:

$$DO_{dw,t+\Delta t} = DO_{up,t} + \frac{\left(\frac{GPP(I)\Delta t}{z}\right) - \left(\frac{ER(T)\Delta t}{z}\right) + K_2(T)\Delta t\left(\frac{DOsat_{up,t} - DO_{up,t} + DOsat_{dw,t+\Delta t}}{2}\right)}{1 + \frac{K_2(T)\Delta t}{2}}$$

where travel time (Δt) is in days, and mean depth (z, meters) is included to obtain metabolism estimates in surface units. $DOsat$ is DO saturation concentration (g m^{-3}), calculated from water temperature and barometric pressure (Hall and Hotchkiss, 2017). The equation denominator is associated with the average DO saturation deficit calculation and the isolation of $DO_{dw,t+\Delta t}$ on one side of the equation (Hall et al., 2016). We modeled GPP as a saturating function of light (Jassby and Platt, 1976):

$$GPP(I) = P_{max}\tanh\left(\frac{\alpha \ I}{P_{max}}\right)$$

where I is the photosynthetic photon flux density (PPFD, µmols photons m^{-2} s^{-1}), α is the slope of the photosynthesis–light relationship at low light intensity, and P_{max} is the photosynthesis rate at light saturation (Fig. A4). We tested the inclusion of temperature dependence of GPP, but did not clearly improve the goodness of fit of the models, so we kept a simpler formulation. We did include temperature dependence of ER (Gulliver and Stefan, 1984):

$$ER(T) = ER_{20} \times 1.045^{T-20}$$

where T is temperature (°C) and ER_{20} is the ecosystem respiration at 20 °C. Temperature also affects air-water O_2 exchange by altering both DO saturation deficit and O_2 exchange coefficient (K_2, day^{-1}). We used Schmidt number scaling to fit models with a coefficient normalized by temperature (i.e. 17.5 °C) and O_2 molecular properties (K_{600}, day^{-1})

(Jähne et al., 1987; Raymond et al., 2012):

$$K_2(T) = K_{600} \times \left(\frac{1568 - 86.04T + 2.142T^2 - 0.0216T^3}{600}\right)^{-0.5}$$

We estimated the posterior distributions of the four parameters (K_{600}, ER_{20}, α and P_{max}) at once by fitting a non-linear model with the *brm()* function of the brms package (Bürkner, 2015) in R (R Core Team, 2020). We chose weakly informative priors for the parameters: $K_{600} \sim N$ (20,20) for Aarhus and Lille, and $K_{600} \sim N(100,50)$ for Vadsted, after calculating K coefficients with empirical equations (Raymond et al., 2012); $ER_{20} \sim N(7,7)$; $\alpha \sim N(20,20)$ for Aarhus and Lille, and $\alpha \sim N(10, 10)$ for Vadsted; $P_{max} \sim N(7,7)$. We included no predictors for these parameters except for K_{600} in Vadsted, which was high and with intra-day oscillations, and was allowed to vary with time with a smoothing term s (time, K = 24) (Bürkner, 2018). We detected an equifinality problem in one case that resulted in unrealistically low values of K_{600} and ER_{20}, which was addressed by constraining K_{600} prior to ~N (11.5,0.5), in accordance with the coefficients obtained for the same reach at other times and with the empirical calculations (Raymond et al., 2012). We evaluated the fitted models by visually comparing observed and modeled DO data, and estimating prediction accuracy with leave-one-out cross validation (loo R package, Vehtari et al., 2020).

For every model, we used 27 h or 36 h time spans of good DO quality data close to the nutrient release dates. We then calculated GPP and ER for 24 h intervals using the estimated parameters, light and temperature. When several days of good data were available, we fitted different models and finally selected the one with lower predictive error (i.e. lower loo), which were often cloudy days with sunny intervals (Fig. A2). The net ecosystem production (NEP) is calculated as NEP = GPP-ER. Unfortunately, we do not have DO data in Lille impact reach in Wk 3 due to problems with the sensor, so metabolism metrics are not estimated for this period. We calculated metabolism response ratios following the same approach as for uptake ratios described above. An R script with all steps followed along the two-station metabolism fitting and checking process is available online (https://github.com/PauGimenezGrau/TwoStationMetabolismBrms).

2.5. Statistical analysis

To test the overall effects of plant removal across the three streams on hydrological, stream nutrient and metabolic metrics, linear mixed models (LMM) were performed with the function "lme" from the package "nlme" (Pinheiro et al., 2023). The fixed structure of the LMM included period (Before/After) and reach (Control/Impact) and the interaction between them (BA:CI), while site was included as random factor. The overall effect of the macrophyte removal on the response variables was assessed according to the significance of the interaction term (BA:CI) between period and reach (Misteli et al., 2023; Pereda et al., 2020). However, this approach was not possible for testing the effects of macrophyte removal on single streams since hydrological, nutrient uptake and metabolism metrics are whole-reach estimates without replicates within reach and time. The p-value = 0.05 was controlled by Bonferroni correction for a set of seven comparisons, including travel time, uptake and metabolism metrics (adjusted p-value = 0.05/7 ≈ 0.00714). All statistical analyses were performed in R (R Core Team, 2020).

3. Results and discussion

3.1. Effects of macrophyte removal on the ecological function of lowland streams

The study streams showed typical characteristics of lowland temperate streams, with low discharge (from 7 to 97 L/s; Table 1) and high nutrient concentrations due to anthropogenic impact (Table 1). We found a 32–78 % decline in ammonium uptake velocity (v_f NH$_4^+$ changed

from 6.6 to 1.5 mm min^{-1} in Aarhus and from 3.2 to 2.2 mm min^{-1} Vadsted) and a 50–77 % decline in phosphate uptake velocity one week after the weed cutting (v_f PO$_4^{3-}$ changed from 5.6 to 1.3 mm min^{-1} in Aarhus and from 5.2 to 2.6 mm min^{-1} Vadsted; Fig. 2). Similarly, areal uptake rates also declined after one week of weed cutting with 35–78 % for ammonium (U NH$_4^+$ from 295.1 to 66.8 µg m^{-2} min^{-1} in Aarhus and 679.3–445.5 µg m^{-2} min^{-1} in Vadsted) and 54–66 % for phosphate (U PO$_4^{3-}$ from 265.8 to 89.2 µg m^{-2} min^{-1} in Aarhus and 366.0–167.4 µg m^{-2} min^{-1} in Vadsted; Fig. 2). These percentages of decrease can be attributed to environmental temporal changes since the control reaches also tended to decrease during the same period (Fig. 2), which could be related to temporal changes of the autotrophic community activity in the stream (Feijoó et al., 2011; Riis et al., 2020b). Nutrient uptake metrics did not significantly change across the three studied streams due to the macrophyte removal (BA:CI, p-value > 0.05, Table 2). However, the

nutrient uptake decreases were not as large as in the impacted reach in Aarhus (not in Vadsted) as shown by the response ratio (Fig. 3). We observed that the response ratio was larger in the reach with weed cutting compared to the control reach (Fig. 3) and, additionally, that the UE ratio for both nutrients declined during the first week after cutting in Aarhus (Fig. 4). These changes indicate high submerged macrophyte activity found in the experimental streams during this period of the year and can be associated to the significant ecological role of macrophytes in lowland streams nutrient cycling (Levi et al., 2015; Riis et al., 2020b).

Our measurements of stream metabolism (GPP: 0.1–4.7 g O$_2$ m^{-2} day^{-1} and ER: 1.3–11.0 g O$_2$ m^{-2} day^{-1}) were within the range previously reported in streams worldwide (Marcarelli et al., 2011) including lowland streams with abundant macrophytes (Alnoee et al., 2021) and displayed the heterotrophic character of the investigated streams (NEP: form −0,03 to - 4.7 g O$_2$ m^{-2} day^{-1}). Interestingly, our metabolic models
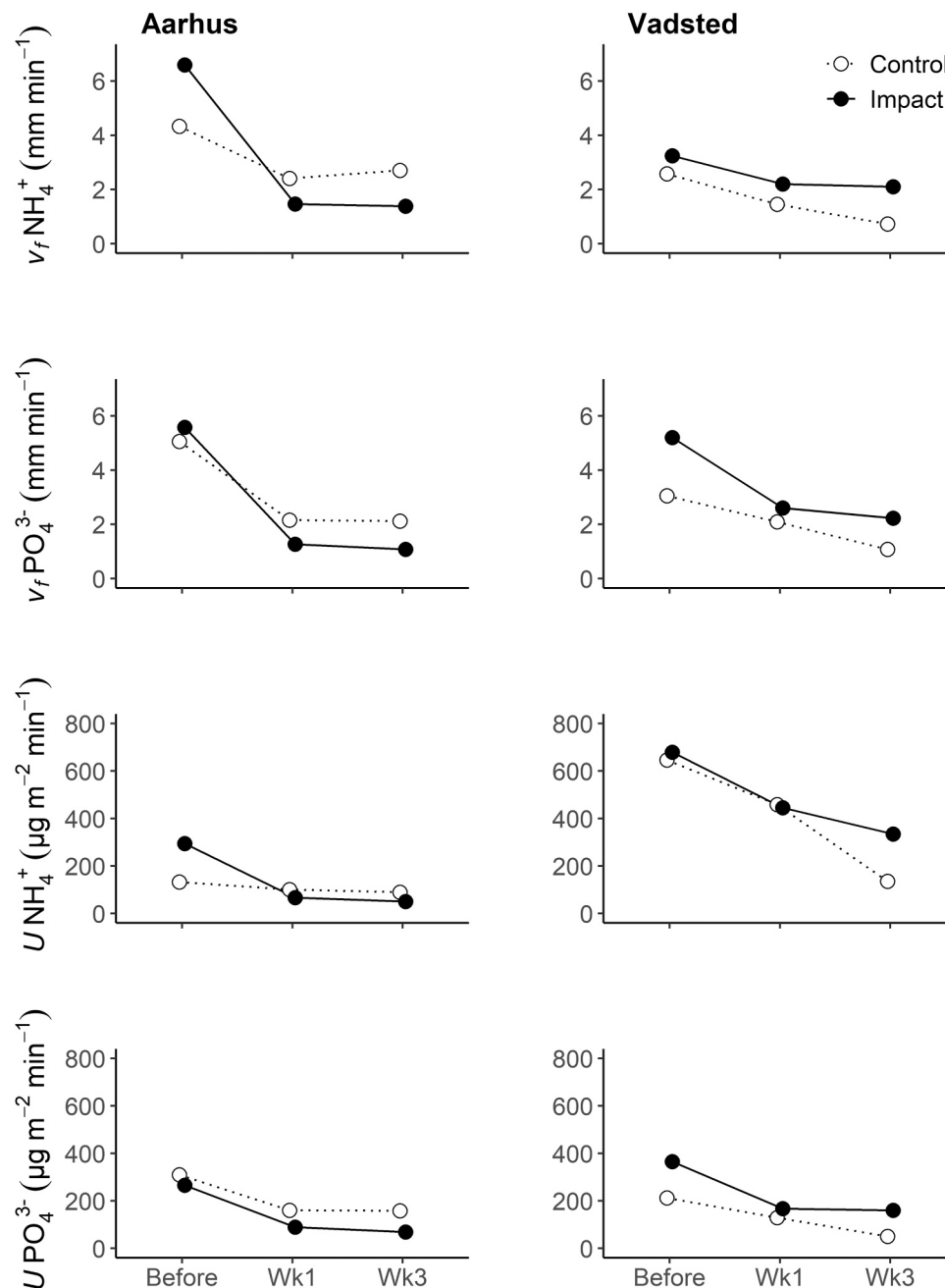

Fig. 2. Nutrient uptake metrics; v_f (mm min^{-1}) and U (µg m^{-2} min^{-1}) in Aarhus and Vadsted for NH$_4^+$ and PO$_4^{3-}$. 'Before' is one week prior to weed cutting, Wk1 and Wk3 is one and three weeks after weed cutting, respectively.

Table 2

Statistical results obtained from linear mixed models to test the effect of macrophyte removal on stream hydrology, nutrient uptake and metabolism variables. The variables included are discharge, travel time, uptake velocity (v_f) and the areal uptake rate (U) for ammonium (NH_4^+) and phosphate (PO_4^{3-}), and gross primary respiration (GPP) and ecosystem respiration (ER). Bold values indicate statistically significant results (Bonferroni adjusted alpha level of $\approx$ 0.007) of the interaction between period and reach (BA:CI). *numDF* and *denDF* represents the degrees of freedom for the numerator and the denominator of the F-statistic, respectively. We ln-transformed U PO_4^{3-} for the model including all data to meet the assumption of normality of the residuals.

		numDF	denDF	F value	p-value
	Travel time	1	12	11.391	0.006
Nutrient uptake	v_f NH_4^+	1	7	1.547	0.254
	v_f PO_4^{3-}	1	7	2.277	0.175
	U NH_4^+	1	7	0.242	0.638
	U PO_4^{3-}	1	7	0.135	0.725
Metabolism	**GPP**	1	10	5.765	0.037
	ER	1	10	14.688	**0.003**

improved when incorporating a light saturation function, but not temperature. We observed that the light intensity at which photosynthesis becomes initially saturated in these streams, as measured from the modeled parameters ($Ik = Pmax/\alpha$), was relatively low, indicating light saturation for stream productivity (Table A4). We found that weed cutting reduced GPP by 60 % and 85 % in the two streams dominated by submerged vegetation (Fig. 5;) and that these reductions were larger than in the control reaches (Fig. 6). However, although the p-value for the BA:CI was <0.05 across streams (BA:CI, p = 0.037, Table 2), this effect was evaluated using a Bonferroni adjusted alpha level of 0.007 and thus not considered statistical significant. Other studies found consistent decreases in GPP after plant removal both in New Zealand (O'Brien et al., 2014), Switzerland (in July but not in May; Kaenel et al., 2000), United States (Madsen et al., 1988) and Denmark (Manolaki et al., 2022; Simonsen and Harremoës, 1978), which show the significant role of macrophytes in unshaded and nutrient-rich streams (Alnoee et al., 2016, 2021).

In agreement with our predictions, ER decreased after weed cutting in all stream reaches (47 −76 % after first week; Fig. 5; BA:CI, p = 0.003, Table 2), and the reductions were larger than in the control reaches, showing the direct negative effect of weed cutting on respiration (i.e. less oxygen consumption) due to the removal of macrophyte autotrophic respiration (Fig. 6). Moreover, decline of ER can also be linked to both an increase in the mobilization and export of fine degradable particles and a reduction of the surface area available for benthic growth (Wijewardene et al., 2022). Previous studies have also identified a decrease in respiration after macrophyte removal (Kaenel et al., 2000; Kurz et al., 2017; Madsen et al., 1988; but not in O'Brien et al., 2014). Interestingly, we observed that the weed cutting effects were more pronounced on ER than on GPP, hence stream reaches become more autotrophic with weed cutting (i.e. NEP in 'Before' < NEP in 'Wk1'; Table A3). This counterintuitive observation indicates the importance of macrophytes to stream respiration, not only directly via effects on autotrophic respiration but also indirectly via enhancing heterotrophic respiration by increasing sedimentation of fine particulate matter, aeration of substrate, and by providing substrate for epihytic microbial communities (Wijewardene et al., 2022).

3.2. Macrophyte growth form modulates the stream response to macrophyte removal

Our study was conducted in three streams that differed in the dominant vegetation growth form in the impacted reach; Aarhus and Lille streams were dominated by submergent plants (*Potamogeton crispus* and *Ranunculus aquatic*) and Vadsted was dominated by the emergent macrophyte *Iris pseudacorus*. We observed some differences in the stream

response after weed cutting which could be attributed to the main macrophyte community in the stream. However, these comparisons should be taken with caution due to the limited number of streams studied, and differences in macrophytes communities among control and impact reach, particularly in Vadsted.

Nutrient uptake rates in the stream dominated by emergent plants (i. e. Vadsted) seem to be less linked to the removal of biomass in comparison to the observations in Aarhus stream, where submergent plants were more common, as shown by three facts. First, the percentage decrease of the nutrient uptake metrics after weed cutting was lower in Vadsted than in Aarhus (Fig. 2). Second, we observed that the response ratio for NH_4^+ uptake velocity in the reach with weed cutting was lower than in the control reach in Vadsted (Fig. 3), indicating no effect of weed cutting. Third, the uptake to export ratio either increased for NH_4^+ or remained constant for PO_4^{3-} in Vadsted (Fig. 4). These findings suggest that weed cutting had limited or no effect on nutrient uptake at this reach, which we attributed to the differences in macrophyte growth form. Both emergent and submerged macrophytes can access nutrients from sediment and water, however the proportion of nutrients obtained from the water should be lower for the emergent plants rooted in sediments and river margins, compared to submergent macrophytes (Pastor et al., 2013, 2014).

For the metabolic rates, GPP was low in all three sampling periods (before and after weed cutting GPP <0.5 g O_2 m^{-2} day^{-1}; Fig. 5) in the stream reach with primarily emergent macrophytes (i.e. Vadsted), which was in accordance with our expectations. This fact reflects the limited contribution of emergent plants to in-stream GPP. We also found that light availability improved following cutting, from 15 mol PAR m^{-2} day^{-1} to above 30 mol PAR m^{-2} day^{-1} (Fig. A3) due to the clearance of the canopy cover by the emergent vegetation. However, the benthic algae community responded only slightly and slowly to this factor since chl a was low (Table 1) and so did GPP (Fig. 6; Fig. A4 for estimated parameters). Furthermore, the response ratio for GPP remained lower than for the control reach and only a slight increase was observed after three weeks being relatively higher than for the control reach (Figs. 5 and 6). The finding that GPP did not increase following weed cutting in Vadsted can reflect an increased mobilization of particulate organic matter previously accumulated at the base of the macrophyte beds, thus increasing the amount of suspended solids in the water column (Sand-Jensen, 1998). In line with that, we observed an increase in water turbidity in Vadsted right after weed cutting that remained high during the studied period (Fig. A5). However, we cannot rule out a change on the mobilized suspended solids upstream due to, for example, changes in hydrology, contributions from the lake or the biogeochemical connectivity with the riparian flow. Contaminants from the upstream wastewater treatment plant upstream could also reduce algal growth (Rosi-Marshall et al., 2013). Taken together, our results might suggest that the limited growth of the benthic algae following weed cutting was associated to increased scouring, reflecting that resuspension of particulate organic matter could have long-term effects on the amount of suspended solids in streams anthropogenic impacted (Ensign and Doyle, 2005; Greer et al., 2017; Rasmussen et al., 2021).

3.3. Limited recovery of stream function three weeks after macrophyte removal

The macrophyte volume three weeks after weed cutting was not recovered to the pre-disturbance conditions for any stream (Table 1). When comparing Wk_1 and Wk_3 after weed cutting, Aarhus was the only stream with a limited increase in macrophyte volume (10 %), which was higher than the control reach (Table 1). A previous comprehensive study in Danish streams showed that macrophyte regrowth after weed cutting (measured in terms of increases in water level) was dependent both on the time and the frequency of the weed cutting at the stream reach (Baattrup-Pedersen et al., 2018). As such, the fastest recovery of macrophytes (ca. 2.5 weeks) happened early summer at streams with high
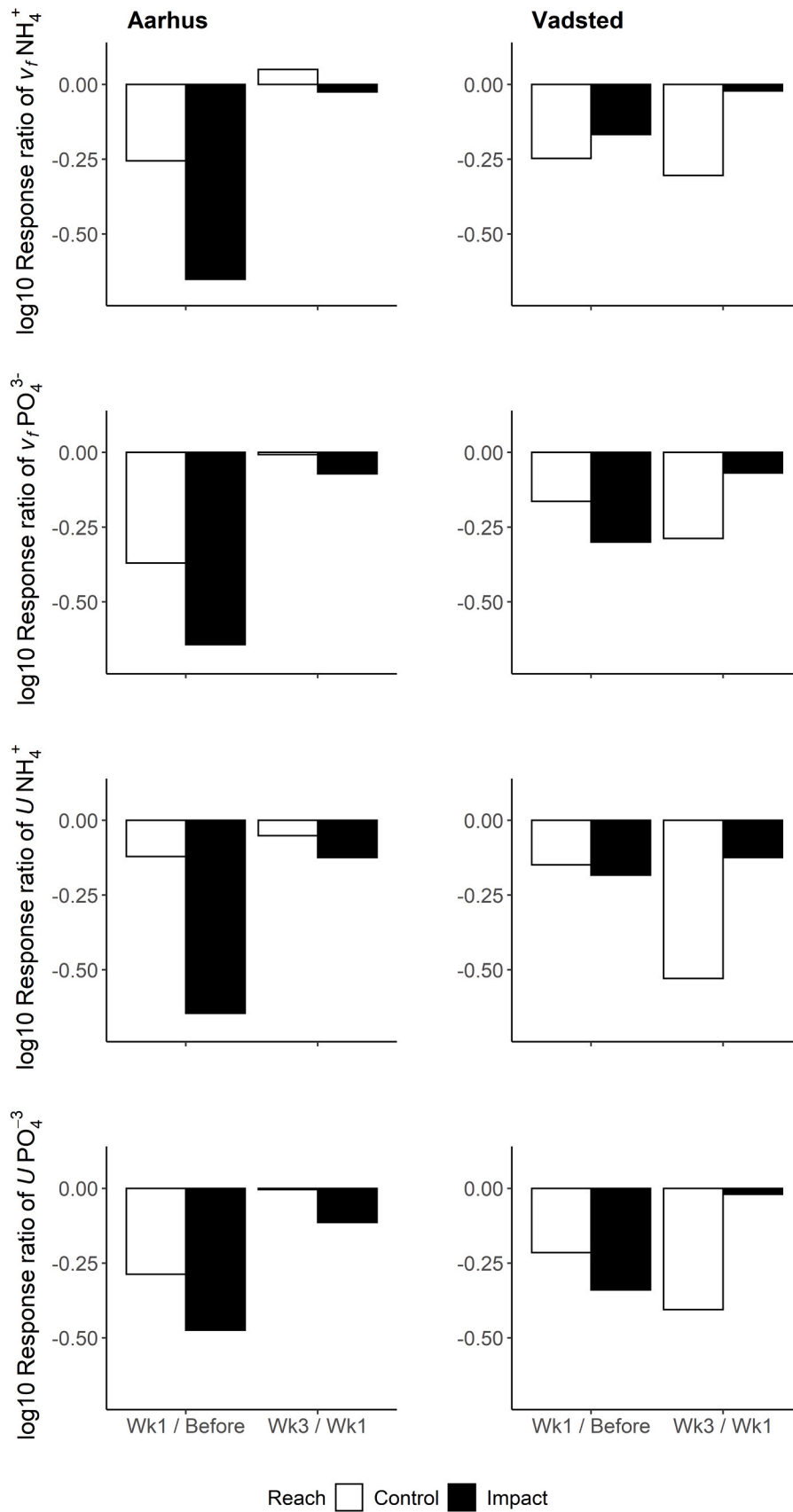
Fig. 3. Nutrient uptake response ratio (log10 transformed) of v_f (gross) and Ugross uptake between Wk 1/ before and Wk 3/Wk 1 for NH_4^+ (top) and PO_4^{3-} (bottom) in Aarhus (left) and Vadsted (right). 'Before' is one week prior to weed cutting, Wk1 and Wk3 is one and three weeks after weed cutting, respectively.
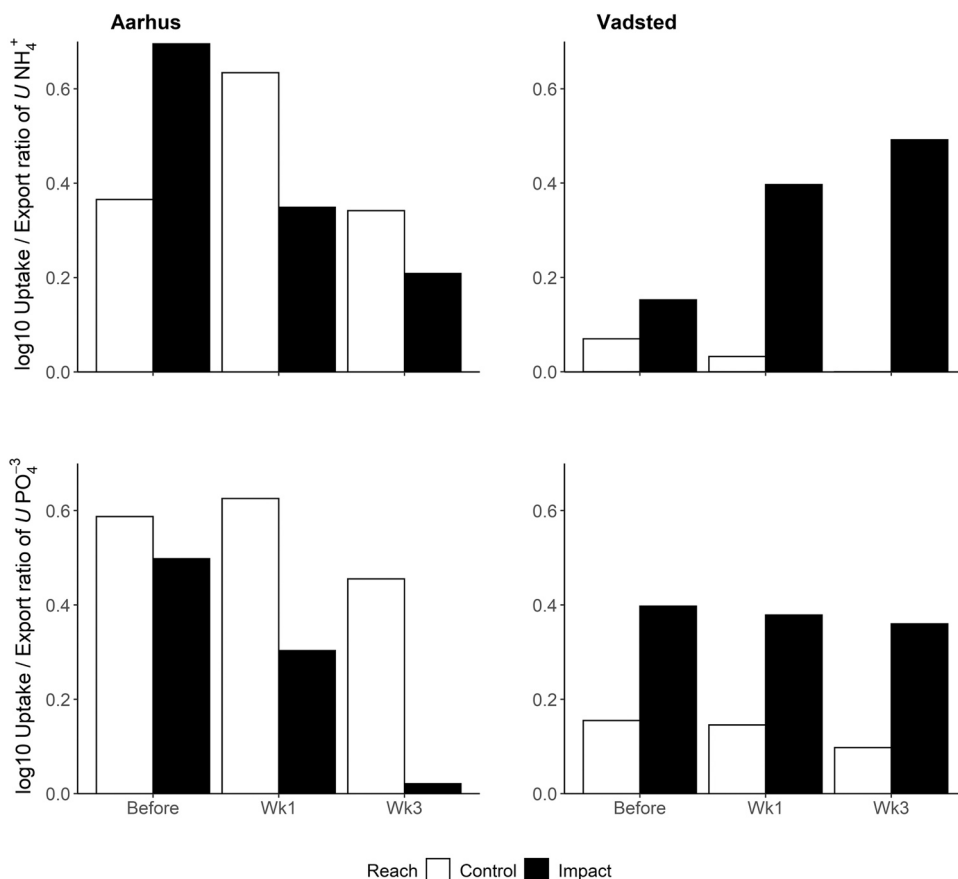
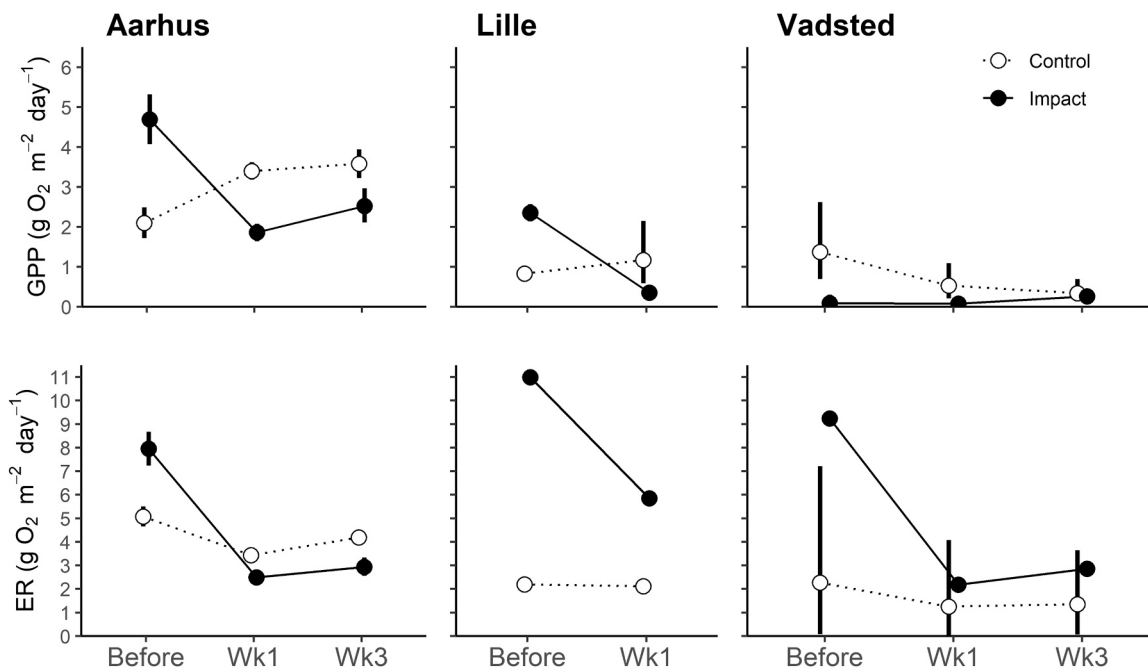**Fig. 4.** Uptake/Export ratio of Ugross (log10 transformed) (dimensionless) for NH_4^+ (top) and PO_4^{3-} (bottom) in Aarhus (left) and Vadsted (right) for the impact reach. A value above 1 indicate uptake is higher than export. 'Before' is one week prior to weed cutting, Wk1 and Wk3 is one and three weeks after weed cutting, respectively.

Fig. 5. In-stream gross primary production (GPP, g O_2 m^{-2} day^{-1}) and respiration (ER, g O_2 m^{-2} day^{-1}) in Aarhus, Lille and Vadsted during the experimental period. 'Before' is one week prior to weed cutting, Wk1 and Wk3 is one and three weeks after weed cutting, respectively. Error bars are the credible intervals of the estimated parameters K_{600}, ER_{20}, α and P_{max}. Any error bar not visible is subsumed within the symbol.
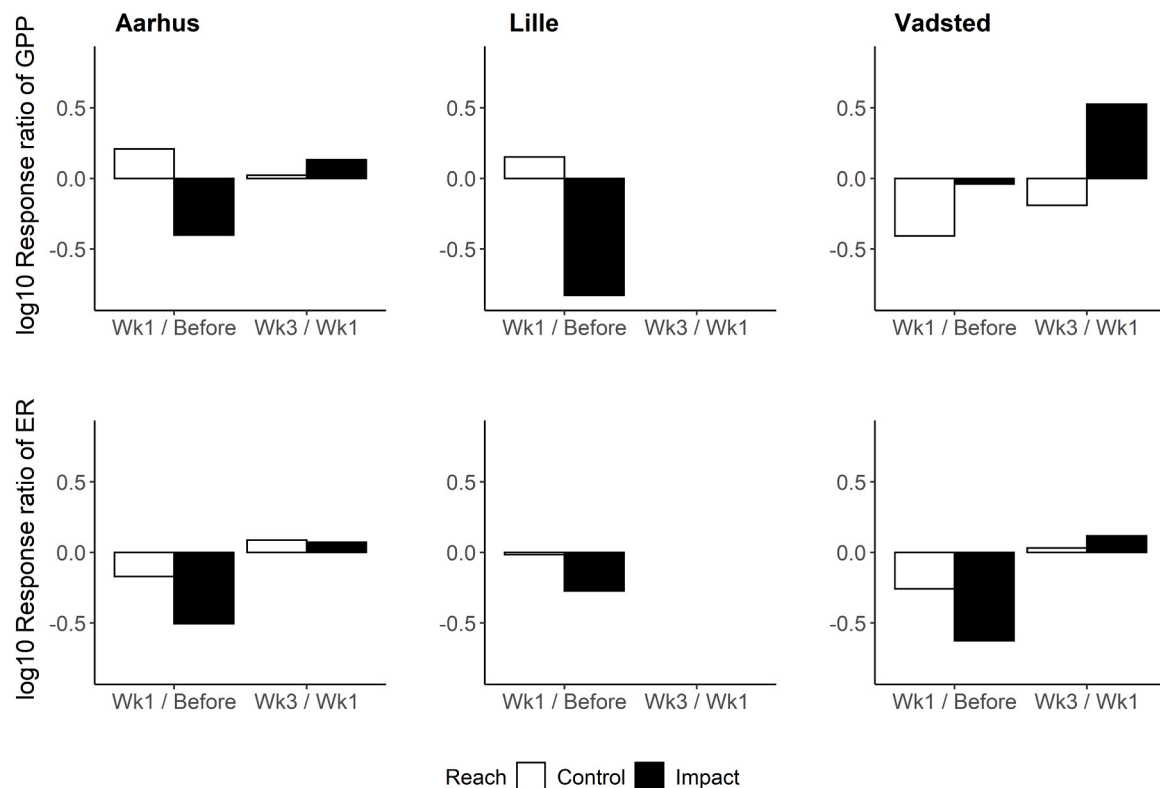
Fig. 6. Metabolism response ratio (log10 transformed) between Wk 1/ before and Wk 3/Wk 1 for GPP (Top) and ER (bottom) in Aarhus (left), Lille (middle) and Vadsted (right). 'Before' is one week prior to weed cutting, Wk1 and Wk3 is one and three weeks after weed cutting, respectively.

weed cutting intensities. In contrast, recovery was absent when weed cutting occurred in autumn. Our study was conducted only for three weeks after weed cutting and limits our interpretations on the macrophyte community beyond this time frame, however we could expect a progressive recovery of macrophyte biomass before autumn starts.

Similarly, to the macrophyte biomass, we did not observe stream nutrient uptake and metabolism to be recovered at the pre-disturbance levels after three weeks of weed cutting (Figs. 2 and 5). These results align with the recent study for a large river in Denmark, where GPP did not recovered pre-cut levels within the 6 weeks period (Manolaki et al., 2022). However, we observed contrasting responses of these stream functions across streams. For nutrient uptake, Aarhus R_{wk3} was lower in the impact reach than in the control reach stream, whereas, in Vadsted, R_{wk3} was higher in the impact reach than in the control reach, which might indicate a slight recovery of the impacted community in this stream. For metabolism, we observed a slight increase in GPP and ER rates in Wk 3 compared to Wk 1 (Fig. 5), with $R_{Wk3} > 0$ that tended to be higher than the control reach for all streams, except ER in Aarhus; Fig. 6). The observed partial rapid recover of stream of metabolic functions, compared to the macrophyte biomass, can be attributed to the growth of benthic algae due to the increase of light availability after macrophyte removal (Kaenel et al., 2000). The monitoring over longer periods would be necessary to further understand the effect of macrophyte senescence and mineralization on stream respiration during autumn.

4. Conclusions

We found that the removal of macrophyte biomass substantially affected nutrient uptake as well as in-stream metabolism, but also that the effect depended on the characteristics of the macrophyte community. Thus, in the reach dominated by submerged vegetation, we found a decline in nutrient uptake, GPP and ER whereas in the reach dominated by emergent vegetation, we only found that nutrient uptake and ER were

reduced but GPP was unaffected. Interestingly, we also observed that the streams became more autotrophic after weed cutting independent of the characteristics of the macrophyte community. Taken together our findings highlight the importance of macrophytes for nutrient cycling in streams and their capacity for reducing the amounts of nutrients transported downstream to the benefit of vulnerable fjords and coastal areas during summer, when they are the most vulnerable to anoxic episodes. We advocate that an improved understanding of how weed cutting affect ecosystem functions in streams is needed to improve management strategies to reduce the flux of nutrients downstream and hence lower the risk of eutrophication.

CRediT authorship contribution

Conceptualization: AP, ABP, TR; Data curation: CMHH, OP, PG-G; Formal analysis: CMHH, OP, PG-G; Funding acquisition: ABP, TR; Investigation: AP, CMHH, OP, PG-G; Methodology: AP, OP, PG-G, TR; Project administration: TR; Resources: TR, ABP; Software: PG-G; Supervision: TR; Visualization: AP, CMHH, PG-G; Roles/Writing - original draft: AP, CMHH, PG-G, TR; Writing - review & editing: AP, CMHH, OP, PG-G, ABP, TR.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: T. Riis and A. Baattrup-Pedersen reports financial support was provided by Velux Foundation. A. Pastor reports financial support was provided by Government of Catalonia.

Data Availability

Data will be made available on request.

Acknowledgments

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.aquabot.2023.103694.

References

Alnoee, A.B., Riis, T., Baattrup-Pedersen, A., 2016. Comparison of metabolic rates among macrophyte and nonmacrophyte habitats in streams. Freshw. Sci. 35, 834–844. https://doi.org/10.1086/687842.

Alnoee, A.B., Levi, P.S., Baattrup-Pedersen, A., Riis, T., 2021. Macrophytes enhance reach-scale metabolism on a daily, seasonal and annual basis in agricultural lowland streams. Aquat. Sci. 83, 11 https://doi.org/10.1007/s00027-020-00766-4.

Álvarez, M., Proia, L., Ruggiero, A., Sabater, F., Butturini, A., 2010. A comparison between pulse and constant rate additions as methods for the estimation of nutrient uptake efficiency in-streams. J. Hydrol. 388, 273–279. https://doi.org/10.1016/j.jhydrol.2010.05.006.

Audet, J., Olsen, T.M., Elsborg, T., Baattrup-Pedersen, A., Riis, T., 2021. Influence of plant habitats on denitrification in lowland agricultural streams. J. Environ. Manag. 286 https://doi.org/10.1016/j.jenvman.2021.112193, 112193–112193.

Baattrup-Pedersen, A., Larsen, S.E., Riis, T., 2002. Long-term effects of stream management on plant communities in two Danish lowland streams. Hydrobiologia 481, 33–45. https://doi.org/10.1023/A:1021296519187.

Baattrup-Pedersen, A., Larsen, S.E., Riis, T., 2003. Composition and richness of macrophyte communities in small Danish streams - influence of environmental factors and weed cutting. Hydrobiologia 495, 171–179. https://doi.org/10.1023/A:1025442017837.

Baattrup-Pedersen, A., Ovesen, N.B., Larsen, S.E., Andersen, D.K., Riis, T., Kronvang, B., Rasmussen, J.J., 2018. Evaluating effects of weed cutting on water level and ecological status in Danish lowland streams. Freshw. Biol. 652–661. https://doi.org/10.1111/fwb.13101.

Balestrini, R., Delconte, C., Palumbo, M., Buffagni, A., 2018. Biotic control of in-stream nutrient retention in nitrogen-rich springs (Po Valley, Northern Italy. Ecol. Eng. 122, 303–314. https://doi.org/10.1016/j.ecoleng.2018.08.014.

Bowden, W.B., Glime, J.M., Riis, T., 2017. Macrophytes and bryophytes. In: Hauer, F.R., Lamberti, G.A. (Eds.), Methods in Stream Ecology. Elesvier, Oxford, pp. 243–272.

Bürkner, P.C., 2018. Advanced Bayesian multilevel modeling with the R package brms. R. J. 10, 395–411. https://doi.org/10.32614/RJ-2018-017.

Bürkner, P.-C., 2015. brms: An R package for Bayesian Generalized Linear Mixed Models using Stan. URL: https://cran.r-project.org/web/packages/brms/ vignettes/brms.pdf [WWW Document].

Carpenter, S.R., Lodge, D.M., 1986. Effects of submersed macrophytes on ecosystem processes. Aquat. Bot. 26, 341–370. https://doi.org/10.1016/0304-3770(86)90031-8.

Clarke, S.J., 2002. Vegetation growth in rivers: influences upon sediment and nutrient dynamics. Prog. Phys. Geogr. 26, 159–172. https://doi.org/10.1191/0309133302pp324ra.

R. Core Team, 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Ensign, S.H., Doyle, M.W., 2005. In-channel transient storage and associated nutrient retention: evidence from experimental manipulations. Limnol. Oceanogr. 50, 1740–1751. https://doi.org/10.4319/lo.2005.50.6.1740.

Feijóo, C., Giorgi, A., Ferreiro, N., 2011. Phosphate uptake in a macrophyte-rich Pampean stream. Limnologica 41, 285–289. https://doi.org/10.1016/j.limno.2010.11.002.

Gordon, N.D., 2004. Stream hydrology: an introduction for ecologists: Nancy D. Gordon et al., 2nd ed. Wiley, Chichester.

Greer, M.J.C., Hicks, A.S., Crow, S.K., Closs, G.P., 2017. Effects of mechanical macrophyte control on suspended sediment concentrations in streams. N. Zeal. J. Mar. Freshw. Res. 51, 254–278. https://doi.org/10.1080/00288330.2016.1210174.

Gulliver, J.S., Stefan, H.G., 1984. Stream productivity analysis with DORM-II. Parameter estimation and sensitivity. Water Res. 18, 1577–1588. https://doi.org/10.1016/0043-1354(84)90134-9.

Hall, R.O., Hotchkiss, E.R., 2017. Stream metabolism. In: Lamberti, G.A., Hauer, F.R. (Eds.), Methods in Stream Ecology. Elsevier, pp. 219–233.

Hall, R.O., Tank, J.L., Baker, M.A., Rosi-Marshall, E.J., Hotchkiss, E.R., 2016. Metabolism, gas exchange, and carbon spiraling in rivers. Ecosystems 19, 73–86. https://doi.org/10.1007/s10021-015-9918-1.

Hussner, A., Stiers, I., Verhofstad, M.J.J.M., Bakker, E.S., Grutters, B.M.C., Haury, J., Valkenburg, J.L.C.H., Van, Brundu, G., Newman, J., Clayton, J.S., Anderson, L.W.J., Hofstra, D., 2017. Management and control methods of invasive alien freshwater aquatic plants: A review. Aquat. Bot. 136, 112–137. https://doi.org/10.1016/j.aquabot.2016.08.002.

Jähne, B., Münnich, K.O., Bösinger, R., Dutzi, A., Huber, W., Libner, P., 1987. On the parameters influencing air-water gas exchange. J. Geophys. Res. 92 (C2), 1937–1949. https://doi.org/10.1029/JC092iC02p01937.

Jassby, A.D., Platt, T., 1976. Mathematical formulation of the relationship between photosynthesis and light for phytoplankton. Limnol. Oceanogr. 21, 540–547. https://doi.org/10.4319/lo.1976.21.4.0540.

Jones, C.G., Lawton, J.H., Shachak, M., 1994. Organisms as ecosystem engineers. Oikos 69, 373–386. https://doi.org/10.2307/3545850.

Kaenel, B.R., Buehrer, H., Uehlinger, U., 2000. Effects of aquatic plant management on stream metabolism and oxygen balance in streams. Freshw. Biol. 45, 85–95. https://doi.org/10.1046/j.1365-2427.2000.00618.x.

Kurz, M.J., Drummond, J.D., Martí, E., Zarnetske, J.P., Lee-Cullin, J., Klaar, M.J., Folegot, S., Keller, T., Ward, A.S., Fleckenstein, J.H., Datry, T., Hannah, D.H., Krause, S., 2017. Impacts of water level on metabolism and transient storage in vegetated lowland rivers - insights from a mesocosm study. J. Geophys. Res. Biogeosci. 122, 628–644. https://doi.org/10.1002/2016JG003695.

Levi, P.S., McIntyre, P.B., 2020. Ecosystem responses to channel restoration decline with stream size in urban river networks. Ecol. Appl. 30 https://doi.org/10.1002/eap.2107 e02107-N./a.

Levi, P.S., Riis, T., Alnoee, A.B., Peipoch, M., Maetzke, K., Bruus, C., Baattrup-Pedersen, A., 2015. Macrophyte complexity controls nutrient uptake in lowland streams. Ecosystems 18, 914–931. https://doi.org/10.1007/s10021-015-9872-y.

Madsen, J.D., Adams, M.S., Ruffier, P., 1988. Harvest as control for Sago Pondweed (*Potamogeton pectinatus* L.) in Badfish Creek, Wisconsin: Frequency, efficiency and its impact on the stream community oxygen metabolism. J. Aquat. Plant Manag. 26, 20–25.

Madsen, T.V., Cedergreen, N., 2002. Sources of nutrients to rooted submerged macrophytes growing in a nutrient-rich stream. Freshw. Biol. 47 (2), 283–291. https://doi.org/10.1046/j.1365-2427.2002.00802.x.

Manolaki, P., Gimenez-Grau, P., Pastor, A., Baattrup-Pedersen, A., Riis, T., 2022. Weed cutting in a large river reduces ecosystem metabolic rates in the case of River Gudenå (Denmark). J. Environ. Manag. 314, 115014.

Manolaki, P., Mouridsen, M.B., Nielsen, E., Olesen, A., Jensen, S.M., Lauridsen, T.L., Baattrup-Pedersen, A., Sorrell, B.K., 2020. A comparison of nutrient uptake efficiency and growth rate between different macrophyte growth forms. J. Environ. Manage. Journal of Environmental Management 274, 111181. https://doi.org/10.1016/j.jenvman.2020.111181.

Marcarelli, A.M., Baxter, C.V., Mineau, M.M., Hall, R.O., 2011. Quantity and quality: unifying food web and ecosystem perspectives on the role of resource subsidies in freshwaters. Ecology 92, 1215–1225.

Martí, E., Sabater, F., 2009. Retencion de nutrientes en ecosistemas fluviales. In: Elosegui, A., Sabater, S. (Eds.), Conceptos y Técnicas En Ecología Fluvial. Fundacion BBVA, pp. 117–132.

Misteli, B., Pannard, A., Aasland, E., Faye, S., Motitsoe, S., Thiemer, K., Coetzee, J., Hilt, S., Jan, K., 2023. Short-term effects of macrophyte removal on aquatic biodiversity in rivers and lakes. J. Environ. Manag. 325, 116442 https://doi.org/10.1016/j.jenvman.2022.116442.

Myrstener, M., 2020. The Role of Nutrients for Stream Ecosystem Function in Arctic Landscapes Drivers of Productivity under Environmental Change. PhD thesis. Umeå Universitet.

O'Brien, J.M., Lessard, J.L., Plew, D., Graham, S.E., McIntosh, A.R., 2014. Aquatic macrophytes alter metabolism and nutrient cycling in lowland streams. Ecosystems 17, 405–417. https://doi.org/10.1007/s10021-013-9730-8.

Pan, Y., García-Girón, J., Iversen, L.L., 2023. Global change and plant-ecosystem functioning in freshwaters. Trends Plant Sci. 1–15. https://doi.org/10.1016/j.tplants.2022.12.013.

Pastor, A., Riera, J.L., Peipoch, M., Cañas, L., Ribot, M., Gacia, E., Martí, E., Sabater, F., 2014. Temporal variability of nitrogen stable isotopes in primary uptake compartments in four streams differing in human impacts. Environ. Sci. Technol. 48 (12), 6612–6619. https://doi.org/10.1021/es405493k.

Pastor, A., Peipoch, M., Cañas, L., Chappuis, E., Ribot, M., Gacia, E., Riera, J.L., Martí, E., Sabater, F., 2013. Nitrogen stable isotopes in primary uptake compartments across streams differing in nutrient availability. Environ. Sci. Technol. 47 (18), 10155–10162. https://doi.org/10.1021/es400726e.

Pereda, O., Solagaistua, L., Atristain, M., de Guzmán, I., Larrañaga, A., von Schiller, D., Elosegi, A., 2020. Impact of wastewater effluent pollution on stream functioning: a whole-ecosystem manipulation experiment. Environ. Pollut. 258. https://doi.org/10.1016/j.envpol.2019.113719.

Pinheiro, J., Bates, D., R. Core Team, 2023. nlme: Linear and Nonlinear Mixed Effects Models.

Preiner, S., Dai, Y., Pucher, M., Reitsema, R.E., Schoelynck, J., Meire, P., Hein, T., 2020. Effects of macrophytes on ecosystem metabolism and net nutrient uptake in a groundwater fed lowland river. Sci. Total Environ. 721. https://doi.org/10.1016/j.scitotenv.2020.137620.

Rasmussen, J.J., Kallestrup, H., Thiemer, K., Baisner Alnøe, A., Dalsgaard Henriksen, L., Larsen, S.E., Baattrup-Pedersen, A., 2021. Effects of different weed cutting methods on physical and hydromorphological conditions in lowland streams. Knowl. Manag. Aquat. Ecosyst. https://doi.org/10.1051/kmae/2021009.

Raymond, P.A., Zappa, C.J., Butman, D., Bott, T.L., Potter, J., Mulholland, P., Laursen, A. E., Mcdowell, W.H., Newbold, D., 2012. Scaling the gas transfer velocity and hydraulic geometry in streams and small rivers. Fluid Environ. 4, 41–53. https://doi. org/10.1215/21573689-1597669.

Reichert, P., Uehlinger, U., Acuña, V., 2009. Estimating stream metabolism from oxygen concentrations: effect of spatial heterogeneity. J. Geophys. Res. Biogeosci. 114, 1–15. https://doi.org/10.1029/2008JG000917.

Riis, T., Sand-Jensen, K., Larsen, S.E., 2001. Plant distribution and abundance in relation to physical conditions and location within Danish stream systems. Environ. Res. 448, 217–228. https://doi.org/10.1023/A:1017580424029.

Riis, T., Dodds, W.K., Kristensen, P.B., Baisner, A.J., 2012. Nitrogen cycling and dynamics in a macrophyte-rich stream as determined by a release. Freshw. Biol. 57, 1579–1591. https://doi.org/10.1111/j.1365-2427.2012.02819.x.

Riis, T., Kelly-Quinn, M., Aguiar, F.C., Manolaki, P., Bruno, D., Bejarano, M.D., Clerici, N., Fernandes, M.R., Franco, J.C., Pettit, N., Portela, A.P., Tammeorg, O., Tammeorg, P., Rodríguez-González, P.M., Dufour, S., 2020a. Global overview of ecosystem services provided by riparian vegetation. Bioscience 70, 501–514. https://doi.org/10.1093/biosci/biaa041.

Riis, T., Tank, J.L., Reisinger, A.J., Aubenau, A., Roche, K.R., Levi, P.S., Baattrup-Pedersen, A., Alnoee, A.B., Bolster, D., 2020b. Riverine macrophytes control seasonal nutrient uptake via both physical and biological pathways. Freshw. Biol. 65, 178–192. https://doi.org/10.1111/fwb.13412.

Rosi-Marshall, E.J., Kincaid, D.W., Bechtold, H.A., Royer, T.V., Rojas, M., Kelly, J.J., 2013. Pharmaceuticals suppress algal growth and microbial respiration and alter bacterial communities in stream biofilms. Ecol. Appl. 23, 583–593.

Sand-Jensen, K., 1998. Influence of submerged macrophytes on sediment composition and near-bed flow in lowland streams. Freshw. Biol. 39, 663–679. https://doi.org/ 10.1046/j.1365-2427.1998.00316.x.

Sand-Jensen, K., 1998. Influence of submerged macrophytes on sediment composition and near-bed flow in lowland streams. Freshw. Biol. 39, 663–679. https://doi.org/ 10.1046/j.1365-2427.1998.00316.x.

Sand-Jensen, K., Riis, T., Martinsen, K.T., 2022. Photosynthesis, growth, and distribution of plants in lowland streams—A synthesis and new data analyses of 40 years research. Freshw. Biol 67 (7), 1255–1271.

Simonsen, J.F., Harremoës, P., 1978. Oxygen and pH fluctuations in rivers. Water Res. 12, 477–489. https://doi.org/10.1016/0043-1354(78)90155-0.

Song, C., Dodds, W.K., Trentman, M.T., Rüegg, J., Ballantyne, F., 2016. Methods of approximation influence aquatic ecosystem metabolism estimates. Limnol. Oceanogr. Methods 14, 557–569. https://doi.org/10.1002/lom3.10112.

Tank, J.L., Rosi-Marshall, E.J., Baker, M. a, Hall, R.O., 2008. Are rivers just big streams? A pulse method to quantify nitrogen demand in a large river. Ecology 89, 2935–2945. https://doi.org/10.1890/07-1315.1.

Thiemer, K., Schneider, S.C., Demars, B.O.L., 2021. Mechanical removal of macrophytes in freshwater ecosystems: Implications for ecosystem structure and function. Sci. Total Environ. 782, 146671 https://doi.org/10.1016/j.scitotenv.2021.146671.

Thomaz, S.M., 2021. Ecosystem services provided by freshwater macrophytes. Hydrobiologia 1–21. https://doi.org/10.1007/s10750-017-3139-x.

Underwood, A.J., 1991. Beyond BACI: experimental designs for detecting human environmental impacts on temporal variations in natural populations. Mar. Freshw. Res. 42, 569–587. https://doi.org/10.1071/MF9910569.

Vehtari, A., Gabry, J., Magnusson, M., Yao, Y., Bürkner, P., Paananen, T., Gelman, A., 2020. loo: Efficient leave-one-out cross-validation and WAIC for Bayesian models.

Wijewardene, L., Wu, N., Fohrer, N., Riis, T., 2022. Epiphytic biofilms in freshwater and interactions with macrophytes: current understanding and future directions. Aquat. Bot. 176, 103467 https://doi.org/10.1016/j.aquabot.2021.103467.