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# Submerged macrophytes affect the temporal variability of aquatic ecosystems

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► **To cite this version:**

Moritz D Lürig, Rebecca J Best, Vasilis Dakos, Blake Matthews. Submerged macrophytes affect the temporal variability of aquatic ecosystems. *Freshwater Biology*, 2021, 66 (3), pp.421-435. 10.1111/fwb.13648 . hal-03373692

**HAL Id: hal-03373692**

**<https://hal.science/hal-03373692>**

Submitted on 13 Oct 2021

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1 **Submerged macrophytes affect the temporal variability of aquatic**  
2 **ecosystems**

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5 Running head: Macrophytes affect variability of ecosystems

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## 20 **Abstract**

- 21 1. Submerged macrophytes are important foundation species that can strongly influence  
22 the structure and functioning of aquatic ecosystems, but only little is known about the  
23 temporal variation and the timescales of these effects (i.e. from hourly, daily, to  
24 monthly).
- 25 2. Here, we conducted an outdoor experiment in replicated mesocosms (1000 L) where  
26 we manipulated the presence and absence of macrophytes to investigate the temporal  
27 variability of their ecosystem effects. We measured several parameters (chlorophyll-a,  
28 phycocyanin, dissolved organic matter [DOM], and oxygen) with high-resolution  
29 sensors (15 min intervals) over several months (94 days from spring to fall), and  
30 estimated metabolic rates of each replicate ecosystem in a Bayesian framework.
- 31 3. Over the entire experiment, macrophytes had a negative effect on phytoplankton  
32 biomass, a positive effect on mean DOM concentration, and either a weak or no effect  
33 on mean metabolic rates, DOM composition, and conductivity. We also found that  
34 macrophytes increased the variance of DOC composition and metabolic rates, and, at  
35 some times of the year, increased the variance of phytoplankton biomass and  
36 conductivity. The observation that macrophytes decreased the mean but increased the  
37 variance of phytoplankton biomass is consistent with a model of competitive  
38 interactions between macrophytes and phytoplankton that we implemented here.
- 39 4. Our high-resolution time series embedded within a manipulative experiment reveal  
40 how a foundation species can affect ecosystem properties and processes that have  
41 characteristically different timescales of response to environmental variation.  
42 Specifically, our results show how macrophytes can affect short-term dynamics of  
43 algal biomass, while also affecting the seasonal buildup of DOM and the variance of  
44 ecosystem metabolism.

## 45 **Introduction**

46 Decades of research on submerged macrophytes have documented how these aquatic plants  
47 can influence a suite of ecosystem properties and processes (Carpenter & Lodge, 1986;  
48 Jeppesen *et al.*, 1997; Huss & Wehr, 2004; Reitsema, Meire & Schoelynck, 2018). Acting as  
49 foundation species (Dayton, 1972; Ellison *et al.*, 2005), macrophytes create and maintain  
50 habitats for other species, affect species interactions, and influence the dynamics of matter  
51 and energy in freshwater ecosystems (Carpenter & Lodge, 1986; Jeppesen *et al.*, 1997).  
52 Populations of individual macrophyte species, as well as species assemblages, can also  
53 influence how aquatic ecosystems respond to environmental change and the propensity of  
54 ecosystems to shift between alternative stable states in shallow lakes (Scheffer *et al.*, 1993;  
55 Blindow, Hargeby & Andersson, 1998; Faafeng & Mjelde, 1998). Importantly, while the net  
56 ecosystem effects of macrophytes in contrasting equilibrium states are well studied, much  
57 less is known about how macrophytes affect the temporal dynamics of ecosystem properties  
58 and processes over timescales ranging from hours, to days, to months (Mitchell & Rogers,  
59 1985; Madsen & Adams, 1988; Iacarella *et al.*, 2018). High-resolution times series that  
60 capture both mean and variance responses of aquatic ecosystems are essential for predicting  
61 the effects of environmental change on aquatic ecosystems (Reitsema *et al.*, 2018; Hillebrand  
62 *et al.*, 2018) and improving their management in light of increasing disturbance and climate  
63 variability (Spears *et al.*, 2017).

64         The strong and persistent ecosystem effects of macrophyte communities are often  
65 linked to their competitive interactions with phytoplankton communities for dissolved  
66 nutrients and light (Carpenter & Lodge, 1986; Scheffer *et al.*, 1993). In shallow lakes, the  
67 positive feedback between light transmission and macrophyte biomass is an important reason  
68 why macrophytes help maintain a clear water state over a wide range of nutrient loading  
69 (Scheffer *et al.*, 1993, 2003; Blindow *et al.*, 1998). Many types of macrophytes are efficient

70 at taking up nutrients from the water and, if rooted, from the sediment, which can limit  
71 phytoplankton growth at low to intermediate nutrient loading (Yamamichi *et al.*, 2018).  
72 Furthermore, macrophytes can reduce fish predation pressure on the zooplankton  
73 communities that graze on phytoplankton (Jeppesen *et al.*, 1997), and can also produce  
74 allelopathic chemicals that inhibit phytoplankton growth (Gross, 2003; Hilt & Gross, 2008;  
75 Nakai *et al.*, 2012). While it is known that such mechanisms can contribute to the positive  
76 feedbacks that help maintain lakes in a clear water state, (Kéfi, Holmgren & Scheffer, 2016;  
77 Iacarella *et al.*, 2018) surprisingly little is known about the seasonal dynamics of these  
78 interactions, partly because (Carpenter, 1988; Benedetti-Cecchi, 2003) to capture variability  
79 of phytoplankton communities over time and concurrently with other ecosystem properties.  
80 This is a problematic knowledge gap because the variance of ecosystem properties is  
81 increasingly recognized as an important dimension of overall ecosystem resilience  
82 (Cottingham & Carpenter, 1998; Benedetti-Cecchi, 2003; Scheffer *et al.*, 2009; Vasseur *et*  
83 *al.*, 2014; Zelnik, Arnoldi & Loreau, 2018).

84 In addition to the effects on phytoplankton dynamics, macrophytes are known to  
85 affect the amount and composition of dissolved organic dissolved organic matter (DOM)  
86 (Bolan *et al.*, 2011; Kellerman *et al.*, 2015), which is a diverse mixture of low and high  
87 molecular weight components of different structure and composition (Bolan *et al.*, 2011;  
88 Kellerman *et al.*, 2015). In the clear water state, phototrophic organisms such as macrophytes,  
89 phytoplankton and bacteria produce low weight dissolved organic carbon (DOC) compounds  
90 such as carbohydrates that are byproducts of photosynthesis (Carpenter & Lodge, 1986;  
91 Retamal *et al.*, 2007; Bolan *et al.*, 2011; Reitsema *et al.*, 2018). Macrophytes can both  
92 directly produce DOC, and indirectly reduce it by stimulating higher rates of DOC  
93 degradation from epiphytic bacteria (Catalán, Obrador & Pretus, 2014). Given the importance  
94 of interactions between macrophytes and different compositions of DOM in aquatic

95 ecosystems (Reitsema *et al.*, 2018) it is important to experimentally test how macrophytes can  
96 simultaneously affect the mean and variance of DOM concentration and composition  
97 (Findlay & Sinsabaugh, 2003; Catalán *et al.*, 2014; Reitsema *et al.*, 2018), and to consider  
98 such effects in models of ecosystem resilience to nutrient perturbation (Kéfi *et al.*, 2016;  
99 Spears *et al.*, 2017).

100         DOM dynamics driven by competitive interactions between macrophytes and  
101 phytoplankton can also alter ecosystem metabolism (Mitchell, 1989; Kaenel, Buehrer &  
102 Uehlinger, 2000; Findlay & Sinsabaugh, 2003; Reitsema *et al.*, 2018). Growth and decay of  
103 macrophyte tissue can strongly affect metabolic rates of shallow lakes, depending on plant  
104 density, diversity and lake depth (Żbikowski *et al.*, 2019). In shallow lakes with a given  
105 nutrient load, ecosystem productivity is typically higher when macrophytes are dominant  
106 over phytoplankton (Wetzel, 1964; Carpenter & Lodge, 1986; Brothers *et al.*, 2013).  
107 Macrophytes are known to be efficient photosynthesizers (Kaenel *et al.*, 2000), but also  
108 provide additional substrate for the growth of autotrophic periphyton and bacteria (Wetzel &  
109 Søndergaard, 1998; Brothers *et al.*, 2013). Additionally, the effects of macrophytes on the  
110 dynamics of DOC accumulation and decomposition can affect shifts between net autotrophy  
111 and net heterotrophy (Mitchell & Rogers, 1985; Madsen & Adams, 1988; Nielsen *et al.*,  
112 2013). Overall, the potential effects of interactions between macrophytes and phytoplankton  
113 on whole ecosystem metabolism are increasingly well documented. However, the ability of  
114 macrophytes to resist or moderate perturbations to ecosystem metabolism in the context of  
115 global change depends on the relative importance of the described mechanisms and the  
116 temporal scale on which they each occur (Zelnik *et al.*, 2018). To our knowledge, only a few  
117 studies have investigated the effects of competition for light and nutrients between  
118 macrophytes and phytoplankton on dynamics of DOC and metabolism at the temporal

119 resolution necessary to understand how they interact (Benedetti-Cecchi, 2003; Zelnik *et al.*,  
120 2018).

121 Here, we experimentally tested how macrophytes affect the temporal dynamics of  
122 oligotrophic aquatic ecosystems in 1000L mesocosms over an entire growing season. We  
123 manipulated the presence and absence of a macrophyte assemblage consisting of two  
124 common species, *Myriophyllum spicatum* and *Chara tomentosa*, and quantified several biotic  
125 (two phytoplankton pigments) and abiotic (temperature and conductivity, dissolved oxygen,  
126 dissolved organic matter) properties at high temporal resolution (15 min). We used this data  
127 set to test three hypotheses. First, we predicted that macrophytes would be able to suppress  
128 phytoplankton biomass across seasonal variation in light and temperature. Second, we  
129 predicted that macrophytes would increase overall rates of ecosystem metabolism because  
130 they are known to be efficient photosynthesizers. Third, we predicted that macrophytes would  
131 impact not only mean ecosystem properties such as phytoplankton biomass, DOM, and  
132 metabolism, but also their temporal variance in response to continual changes in resource  
133 availability. For this last hypothesis, we also tested whether we could generate observed  
134 contrasts in variability using a simple model of competitive interactions between  
135 phytoplankton and macrophytes. We compare our findings with previous empirical work and  
136 discuss the broad functional spectrum of macrophytes as foundation species in shallow lake  
137 ecosystems.

## 138 **Material and methods**

### 139 **Experimental design and setup**

140 In an outdoor mesocosm experiment, we manipulated the presence or absence of an  
141 assemblage of macrophytes including *Myriophyllum spicatum* (hereafter *Myriophyllum*), a

142 perennial vascular plant that grows vertically towards the water surface forming a canopy,  
143 and *Chara tomentosa* (hereafter *Chara*), a green algae that forms tufts of calcium carbonate  
144 encrusted stems (typically <30cm) on the sediment surface. We chose this assemblage  
145 because both species are common in Europe and other parts of the world, they commonly  
146 occur together in macrophyte assemblages, and their strong influence on lake ecosystems has  
147 been previously documented (Van den Berg *et al.*, 1998; Ibelings *et al.*, 2007; Hilt & Gross,  
148 2008; Nakai *et al.*, 2012).

149         We set up the experiment on a site next to Eawag Kastanienbaum (eight tanks total)  
150 with four pairs of 1000L mesocosms (1 x 1 x 1 m), with each pair consisting of a mesocosm  
151 with (M+) and without (M-) a macrophyte assemblage (Fig. 1). To prepare the mesocosms,  
152 we first established a 2 cm thick layer of limestone gravel from a local quarry (2-4 mm grain  
153 size) and a 1 cm thick layer of fine, oligotrophic sediment (Fiskal *et al.*, 2019) that we  
154 collected from Lake Lucerne. Afterwards the mesocosms were filled with water from Lake  
155 Lucerne, an oligotrophic lake (Fiskal *et al.*, 2019), and left for two weeks to allow the  
156 sediment to settle and the mesocosm community to assemble. On May 25th, 2015, we  
157 collected *Myriophyllum* from a stream in Oberriet (47°19'55.5"N 9°34'43.9"E), and kept the  
158 plants overnight in additional outdoor mesocosms onsite. The following day we collected  
159 *Chara* from Lake Lucerne (47°00'06.8"N 8°20'02.7"E) and planted both species in the  
160 mesocosms. We then divided all the macrophyte material manually (on a large and moist  
161 plastic sheet) into 18 similar sized portions based on either an equal number of shoots (i.e. for  
162 *Myriophyllum*), or similarly sized tufts (i.e. for *Chara*). We used 10 portions to quantify the  
163 initial plant biomass (cleaned of sediment, infauna removed, biomass dried for 48 hours at  
164 45°C), and added 4 portions to the M+ tanks. To inoculate the M- mesocosms with  
165 macrophyte associated invertebrate and bacterial communities, we submerged the remaining  
166 four portions of macrophytes in large mesh enclosures in the middle of the water column for



167 two weeks. On July 4th, we added 20  $\mu\text{g/L}$  of P and 144.7  $\mu\text{g/L}$  of N (i.e. Redfield ratio) to  
168 every mesocosm to supplement the Lake Lucerne source water with nutrients. Over the  
169 course of the experiment we measured dissolved nutrient concentrations in the mesocosms on  
170 four occasions (July 15, Aug. 5, Sept 8. and Oct 20, Fig. S1). At the end of the experiment  
171 (Oct 23rd) we quantified total macrophyte biomass in terms of above-ground dry weight  
172 (procedure: see above). This included both the original inoculated species and a filamentous  
173 algae species that colonized the sediment surface of all the mesocosms (see Table S1).

#### 174 **Ecosystem dynamics measurement using multiparameter sondes**

175 We measured high-frequency ecosystem dynamics in the mesocosms from July 18th to Oct  
176 23rd, 2015, using four autonomous multi parameter instruments (EXO2 modular sensor  
177 platform [YSI-WTW], hereafter referred to as sondes). The sondes were placed  
178 approximately at the center of the mesocosm ( $\sim 0.5$  m depth), away from the walls and outside  
179 of patches of macrophytes. Additionally, we measured photosynthetically active radiation  
180 (PAR) in 15 min intervals using a quantum sensor (Li-Cor) installed onsite to estimate  
181 surface light irradiance. PAR and sonde temperature data (Fig. S2) were used together with  
182 the dissolved oxygen data to estimate metabolic rates (see *Ecosystem Metabolism Modelling*).  
183 *Sensors* - The sondes were equipped with modular sensors that recorded the following  
184 ecosystem parameters at 15 minute intervals (see Table 1 for details): temperature,  
185 chlorophyll-a and phycocyanin (as proxies for phytoplankton biomass), dissolved oxygen,  
186 fluorescent dissolved organic matter (fDOM) and specific conductivity. The sondes were  
187 equipped with an autonomous wiper that cleaned the sensor heads once every hour. All  
188 sensors were thoroughly cleaned whenever the sondes were moved to another mesocosm (see  
189 *Contrasts and sampling design*).

190 *Calibration* - Prior to the experiment, we performed a 48h cross-comparison trial where we  
191 installed all the sondes in a single mesocosm, enabling us to correct for differences among  
192 sensors and calibrate them against each other. During the cross-comparison trial we also  
193 quantified chlorophyll-a concentration by analyzing water samples with high performance  
194 liquid chromatography (HPLC, Jasco), and calibrated the optical sensors installed on the  
195 sondes in accordance with the manufacturer's manual (YSI-WTW). Hence, we report  
196 chlorophyll-a as  $\mu\text{g/L}$ , Phycocyanin and fDOM as raw fluorescence units. The oxygen  
197 sensors were calibrated against water-saturated air.

198 *Contrasts and sampling design* - At the beginning of the experiment, all four sondes were  
199 randomly assigned to two pairs of M+ and M- tanks. Because we only had four sondes  
200 available, the four sondes were taken out of these tanks after 10 days, thoroughly cleaned,  
201 and then introduced to the two remaining pairs, where they were left for another 10-day  
202 period (Fig. 1). Over the entire study we repeated this two-part cycle five times, yielding five  
203 distinct periods in which all tanks were sampled (Fig. 2-4: t1-t5). On the third sampling  
204 period (t3) we reduced the length of the measurement period to 7 days per set of tanks due to  
205 battery issues with the Sondes. Between all transfers, we thoroughly cleaned the sondes by  
206 hosing down the sondes and sensor bodies with a power washer before reinstalling them. We  
207 included the distinct periods (t1-t5) resulting from the rotation scheme and each individual  
208 tank as a random effect in all statistical models (see *Statistical Analysis*).

### 209 **Ecosystem metabolism estimation**

210 We used the temperature and oxygen measurements (mg/L) from the sondes and the PAR-  
211 measurements from the light sensor to model whole ecosystem metabolic rates of each  
212 mesocosm (for an overview of the abiotic conditions see Fig. S2). We used the  
213 *streamMetabolizer* package (Appling *et al.*, 2018) in the programming language R (R Core

214 Team 2017), which applies inverse modelling to estimate daily rates of gross primary  
215 productivity (P), respiration (R) and gas exchange (K600) as g O<sub>2</sub>/m<sup>2</sup>/day. For every  
216 modelled rate we calculated the ratio of P and R. Prior to modelling we smoothed all input  
217 data with a 12-hour moving average window to facilitate model convergence (A. Appling,  
218 personal communication) and for more conservative estimates. We used a Bayes-type model  
219 with pooled K600 for gas-exchange and lognormal priors (K = 0-1). Because the dissolved  
220 oxygen time series reflects oxygen produced and consumed by all organisms in the whole  
221 ecosystem, we assumed the model reflects the net effects of any biomass changes throughout  
222 the experiment, for example, due to plant or epiphytic growth, or biomass decay.

### 223 **DOC sampling**

224 For each pair of tanks within each measurement period (i.e. every 10 or 7 days: Table S2) we  
225 took a water sample for the analysis of DOC concentration and absorbance properties (Fig.  
226 S3). Water samples were filtered through 47mm ashed GF/Fs (6 hours at 450°C), acidified  
227 with HCl 2 M and preserved at 4°C in the dark until analysis via high temperature catalytic  
228 oxidation (TOC-VCS, Shimadzu), with a detection limit of 0.5 mg/L (±0.5). Specific  
229 ultraviolet absorbances (SUVA) were measured on the same samples from scans (1 nm  
230 intervals) on a Shimadzu UV1700 spectrophotometer, using 1 cm quartz cuvettes. We  
231 selected absorbance at 254 nm (SUVA<sub>254</sub>) as a proxy of aromaticity and reactivity of DOC  
232 (Weishaar *et al.*, 2003). Furthermore, we measured SUVA<sub>350</sub>, which is an indicator for how  
233 much UVA radiation is absorbed in the water (Fischer *et al.*, 2015). We normalized the  
234 SUVA measurements by dividing the sample absorbances by the total DOC concentration  
235 (Hansen *et al.*, 2016). Finally, we calculated spectral slope ratio (SSR) as the ratio of linear  
236 regressions of the log-transformed spectra of 275–295 nm and 350–400 nm (Helms *et al.*,  
237 2008; Hansen *et al.*, 2016). SSR is a common proxy for DOC molecular weight, to which it

238 should be inversely related. We were unable to analyze two DOC timepoints over the course  
239 of the experiment (Oct 2nd, and 17th) due to technical problems with the TOC analyzer.

## 240 **A model for competition between macrophytes and phytoplankton**

241 We used an existing model for competition between macrophytes and phytoplankton  
242 (Scheffer & Carpenter, 2003) to explore how mesocosm phytoplankton dynamics might  
243 differ in the presence and absence of macrophytes. This model assumes standard features of  
244 macrophyte-phytoplankton interactions and implicitly accounts for competition for light and  
245 nutrients (Fig. 5). In the model, growth of macrophytes  $M$  and of phytoplankton  $P$  is  
246 determined by a gain and a loss term following:

247

$$248 \quad \frac{dP}{dt} = r_P \frac{n}{n+h_P} \frac{1}{1+\alpha_P P} P - l_P P + \sigma \varepsilon_P(t) \text{ (eq1a)}$$

$$249 \quad \frac{dM}{dt} = r_M \frac{1}{1+\alpha_M M + b_P P} M - l_M M + \sigma \varepsilon_M(t) \text{ (eq1b)}$$

250 Phytoplankton grows with a maximum growth rate  $r_P$  that is limited by nutrients  $n$  in a  
251 saturating function with half-saturation constant  $h_P$ . Limitation of phytoplankton growth by  
252 macrophytes comes through nutrient availability given by eq2:

$$253 \quad n = \frac{N_{tot}}{1+q_M M + q_P P} \text{ (eq2)}$$

254 where  $N_{tot}$  is the total amount of nitrogen in the system and nutrients decrease in a nonlinear  
255 way depending on the biomass of macrophytes and phytoplankton. Parameters  $q_M$  and  $q_P$   
256 determine the strength of the response in decreasing nutrients per biomass increase in  
257 macrophytes and phytoplankton, respectively. Phytoplankton growth is also limited by light  
258 due to self-shading scaled by  $\alpha_P$  where  $1/\alpha_P$  is the biomass of phytoplankton that makes the  
259 maximum growth rate equal to half, whereas loss is determined by loss rate  $l_P$ . Macrophyte  
260 maximum growth rate  $r_M$  is limited only due to competition for light (in contrast to  
261 phytoplankton which is also limited by nutrients). In that case, light limitation is driven by

262 self-shading through parameter  $a_M$  and due to shading by phytoplankton by parameter  $b$ . Loss  
263 is determined by loss rate  $l_M$ . In this simplified model formulation, we ignore some  
264 potentially important interactions for which we had no empirical data, including nutrient  
265 uptake by macrophytes from the sediment, and interactions between macrophytes and  
266 periphyton biomass over time.

267 We used model parameters such that both macrophytes and phytoplankton were  
268 equivalent in the rates of growth ( $r_P=r_M=0.5$ ), mortality ( $l_P=l_M=0.05$ ), and self-shading  
269 ( $\alpha_P=\alpha_M=0.01$ ). Instead, we modeled asymmetry between macrophytes and phytoplankton in  
270 terms of light and nutrient limitation. Phytoplankton growth was limited by nutrients ( $h_P =$   
271  $0.2$ ), through macrophytes having a stronger impact on retaining the available nutrients in the  
272 water column ( $N_{tot}$ ) ( $q_M = 0.075$  and  $q_P = 0.005$ ). Macrophytes became light limited by  
273 phytoplankton due to shading ( $b = 0.02$ ). We set  $N_{tot}=3.2$ . This is a total nutrient level value  
274 for which the model can give rise to 2 alternative states, one state with both macrophytes and  
275 phytoplankton present (M+) and an alternative with phytoplankton but no macrophytes (M-).  
276 These two states resemble our experimental setup. We simulated model dynamics at these  
277 two contrasting states in the presence of environmental stochasticity  $\varepsilon_P(t)$ ,  $\varepsilon_M(t)$  (iid different  
278 for macrophytes and phytoplankton) with strength  $\sigma$  ( $=0.5$ ). We produced 200 simulated sets  
279 of 1000 timepoints in length for each of the two states using the same sequence of stochastic  
280 realizations for both states. In that way, differences in the recorded standard deviation and  
281 coefficient of variation were independent of the stochasticity and only due to the stability of  
282 the two states. The model was implemented in MATLAB R2016b (Mathworks) using Grind  
283 v2 (<https://www.sparcs-center.org/resources/dynamical-modelling-tools.html>). Equilibria and  
284 eigenvalues were estimated numerically, stochastic equations were solved with Euler-  
285 Murayama integration using a 0.01 step.

286 **Statistical analysis**

287 *Data treatment* - Prior to the statistical analysis we removed incomplete days at the beginning  
288 and end of each measurement period (five time series: t1-t5). After this, each of the five time  
289 series had 864 data points (15 min interval = 96 data points per day = 9 days) for t1-3 and 576  
290 data points (= 6 days) for t4 and t5. In a second step, we identified residuals of the detrended  
291 data that were outside 2.5 times the interquartile range as outliers and removed them from the  
292 data set. Finally, we used sliding windows with a size of 96 timepoints (= 1 day) to calculate  
293 time series of mean and cv, resulting in 768 data points for t1-t3 and 480 data points for t4-t5  
294 (8 and 5 days, respectively).

295 *Ecosystem dynamics* - We analyzed time series of chlorophyll-a, phycocyanin, dissolved  
296 oxygen and fDOM separately for each of the five measurement periods to account for any  
297 variation due to the sonde-switching. To test for effects of macrophytes on the mean and  
298 variance of each parameter we implemented a series of generalized additive models (GAM)  
299 using the R-package *mgcv* (Wood, 2004): one model per parameter (chlorophyll-a,  
300 Phycocyanin, fDOM, oxygen concentration, conductivity) per measurement period (t1-t5) per  
301 metric (mean or CV), resulting in a total of 50 separate GAMs. Each model used data from  
302 all eight tanks to test for differences in the mean or coefficient of variation (CV), with the  
303 presence or absence of macrophytes as the independent variable and tank and pair (see Fig. 1)  
304 as random effects. All GAMs included a term that accounted for first order autocorrelation  
305 and used penalized thin plate regression splines with automatic knot selection.

306 In addition to the GAMs we also calculated pairwise log response ratios (LRR) for  
307 macrophyte presence in all five periods for the high frequency measurements. To do so we  
308 divided vectors of mean and CV (coming either from the sliding window for the water  
309 parameters or from the daily estimates of metabolism) for M+ by the corresponding vector of

310 M- for each given pair of tanks. We then calculated the natural logarithm for these ratios for  
311 each measurement period and for each tank (for a summary of all response ratios see Fig. 6).  
312 *Ecosystem metabolism* - To test for statistical differences in metabolic rates, we used the  
313 output from the ecosystem metabolism models, which were 8 or 5 consecutive days for t1-t3,  
314 and t4-t5, respectively (streamMetabolizer does not provide estimates for the final day in a  
315 time series). In a similar fashion as for the ecosystem dynamics, each model used data from  
316 all eight tanks within a measurement period to test for differences in P, R or P:R, using  
317 macrophyte presence as the independent variable and pair and tank as random effects. We  
318 calculated LRRs in the same way as described for the high frequency ecosystem dynamics.  
319 We used paired t-tests to test for differences in metabolism CV for each measurement period.  
320 *DOC* - We used paired t-tests to test for differences in mean and CV of total DOC  
321 concentration, SUVA<sub>254</sub> and SUVA<sub>350</sub>, and SSR between mesocosms with and without  
322 macrophytes. For each date (10 dates in total, see Table S2) we performed separate tests for  
323 all four metrics (n=8 tanks). We performed t-tests with the *stats* R-package (R Core Team  
324 2017), and calculated pairwise LRRs for all DOC metrics (for a summary of all response  
325 ratios see Fig. 6).

## 326 **Results**

### 327 **Macrophyte biomass and nutrients**

328 The overall biomass of the macrophyte community changed over the course of the  
329 experiment, decreasing in the M+ treatment and increasing slightly in the M- treatment. At  
330 the end of the experiment substantially less *Chara* biomass was present in the M+ mesocosms  
331 than at the beginning (from  $165.1 \pm 21.65$  g to  $5.08 \pm 7.6$  g dry weight/mesocosm, mean  $\pm$  se,  
332 Table S1), whereas *Myriophyllum* biomass increased threefold from  $2.84 \pm 0.54$  g to  $8.45 \pm$

333 1.6 g dry weight (mean  $\pm$  se). In the M- treatment there was no *Myriophyllum*, but *Chara*  
334 biomass increased slightly due to growth from the sediment (from 0 to  $0.27 \pm 0.54$  g dry  
335 weight, mean  $\pm$  se). In both treatments, filamentous algae grew over the course of the  
336 experiment to a final biomass of  $8.33 \pm 10.54$  g dry weight (M+) and  $3.21 \pm 5.46$  g dry  
337 weight (M-, mean  $\pm$  se). Throughout the experiment we observed no differences in  
338 concentrations of phosphate or nitrogen between mesocosms with and without macrophytes  
339 (Figure S1). The nutrients we supplied on July 4th were almost completely consumed by July  
340 18th and were consistently low ( $<2\mu\text{g P/L}$ ,  $<50\mu\text{gN/L}$ ) over the entire experiment. However,  
341 concentrations of both nutrients tended to increase towards the end of the experiment, likely  
342 due to decomposition of plant material (e.g. *Chara*).

### 343 **Ecosystem dynamics**

344 As expected, solar radiation and water temperature decreased strongly over the course of the  
345 experiment from July 18th to Oct 20th (Fig. S2). Several parameters differed between M+  
346 and M- tanks over the course of the experiment, with the magnitude of the difference  
347 depending on period (Fig 2 and Fig. 6; for P-values see Table 2). As expected, mean  
348 phytoplankton biomass was significantly higher without macrophytes (M-) in three of the five  
349 periods (t2, t4, and t5; Table 2), and, unexpectedly, the CV of phytoplankton biomass was  
350 higher in the tanks with macrophytes (M+) in three periods (t1, t2, and t5, Fig. 3). By  
351 comparison, mean phycocyanin was not significantly different between M+ and M- (Fig. 2),  
352 but the CV of phycocyanin was significantly higher in the M+ treatment during three periods  
353 (Fig. 3; t1, t2, t4). In tanks with macrophytes (M+), fDOM was higher in four periods (GAM,  
354 t2 - t5), and the CV was significantly lower in one period (GAM, t3). The mean concentration  
355 of dissolved oxygen was significantly higher in M+, but only towards the end of the  
356 experiment (Fig. 3, t4 and t5). In these two periods when irradiance was decreasing (Fig. S2),



357 the tanks lacking macrophytes (M-) became undersaturated with dissolved oxygen indicating  
358 net heterotrophy. During the entire experiment, there were no differences between M+ and  
359 M- in the CV of dissolved oxygen. Effect sizes of macrophyte presence on mean and variance  
360 of all parameters measured in high frequency are summarized in Figure 6.

### 361 **Ecosystem metabolism**

362 We found weak and seasonally variable differences in mean ecosystem metabolism between  
363 mesocosms with and without macrophytes (Fig. 4). In three measurement periods mesocosms  
364 with macrophytes had significantly higher gross primary productivity (t1, t3, and t5). During  
365 t1, mesocosms with macrophytes also had higher respiration (GAM, main effect of  
366 macrophytes,  $P = 0.001$ ). In t2 there was a tendency for higher P:R ratio in mesocosms  
367 without macrophytes (GAM, main effect of macrophytes,  $P=0.074$ ), but in t3 and t4 we found  
368 the opposite pattern with significantly higher P:R ratio in the presence of macrophytes  
369 (GAM, main effect of macrophytes,  $P<0.001$  and  $P=0.002$ , respectively. Overall, P and R  
370 decreased significantly over the course of the experiment, likely due to seasonal dynamics  
371 (decreasing temperature and light, Fig. S2) but the P:R ratio remained around one. Across all  
372 measurement periods, both productivity and respiration increased with chlorophyll-a biomass  
373 (slope in Fig. S4). However, for a given chlorophyll-a concentration, both metabolic rates  
374 were higher in the presence of macrophytes than in their absence (intercept in Fig. S4).  
375 Moreover, we found higher variance of metabolic rates when macrophytes were present (all t-  
376 tests of metabolism CV significantly different - Fig 6).

### 377 **DOC**

378 Total DOC concentration was not significantly different between M+ and M- mesocosms  
379 (Table S2, Fig. S3). However, there were clear effects of macrophytes on chromophoric  
380 (impacting light transparency) DOC components:  $SUVA_{254}$  and  $SUVA_{350}$  were often higher

381 in the presence of macrophytes (Table S2, Fig. S3), indicating that less UV light was able to  
382 penetrate in these ecosystems. SSR diverged among treatments early in the experiment and  
383 remained higher in the -M treatment for most of the season (Fig. S3), potentially indicating  
384 dissolved substances of lower molecular weight in the absence of macrophytes (e.g. sugars or  
385 amino acids). We also found higher variance in all metrics of DOC composition in the  
386 presence of macrophytes (Fig 6).

### 387 **Simulated interactions between macrophytes and phytoplankton**

388 Our simulation model produced results parallel to those observed in the mesocosms. Under  
389 identical nutrient levels, phytoplankton biomass was on average lower in the presence of  
390 macrophytes, but also varied more strongly around the mean (i.e. lower mean and higher CV  
391 under M-). This was also reflected in the stability regimes measured as the dominant  
392 eigenvalue lambda, which was higher in the absence and lower in the presence of  
393 macrophytes (Fig. 5, panel B). These results emerged solely from differences in the relative  
394 effects of macrophytes vs. phytoplankton on nutrient vs. light limitation and illustrate that  
395 differential competition for these resources can impact both mean and variance in  
396 phytoplankton biomass.

## 397 **Discussion**

398 Over the course of our experiment, macrophytes affected a wide range of ecosystem  
399 parameters. Most notably from those measured at high frequency, chlorophyll-a fluorescence  
400 (i.e. phytoplankton biomass) was significantly lower in the presence of macrophytes. This  
401 was expected, and in agreement with a large body of previous work documenting the  
402 outcome of competition between macrophytes and phytoplankton for dissolved nutrients and  
403 light (Sand-Jensen & Borum, 1991; Scheffer *et al.*, 1993; Faafeng & Mjelde, 1998; van Nes,

404 Rip & Scheffer, 2007). The ability of macrophytes to keep phytoplankton biomass low is  
405 important for stabilizing the clear water state in response to nutrient additions (Scheffer *et al.*,  
406 1993; Ibelings *et al.*, 2007), and for understanding the timescale of competition for light and  
407 nutrients between these producers in the context of ecosystem stability. However, our high-  
408 resolution measurements also revealed some unexpected variance patterns of macrophyte-  
409 ecosystem interactions, most notably higher variance of phytoplankton and DOC components  
410 in the presence of macrophytes. While the former may be explained by resource competition  
411 between macrophytes and phytoplankton, as indicated by our competition simulation, the  
412 mechanisms behind elevated DOC variability are potentially related to growth and  
413 decomposition of macrophytes. Below we discuss the implications of our joint findings from  
414 the high-resolution time series and the simulation model, as well as the outcomes of the  
415 ecosystem metabolism models. Overall, our findings indicate that some macrophyte effects  
416 on ecosystem parameters are of more limited duration (e.g. phytoplankton was decreased  
417 only temporarily and most strongly in t2), whereas others remain stable across the season  
418 (e.g. fDOM was consistently higher from t2 onwards).

419         As expected from existing theoretical and experimental work, and confirming our first  
420 hypothesis, we observed higher phytoplankton biomass in the absence of macrophytes  
421 (Scheffer *et al.*, 1993; Blindow *et al.*, 1998). However, a finding we did not expect based on  
422 existing theory was the higher variability of phytoplankton biomass in the presence of  
423 macrophytes, a phenomenon that has not been previously reported. One mechanism for  
424 higher variability of phytoplankton biomass could be that the ongoing photosynthesis,  
425 growth, and decay of macrophytes increases the short-term variability of nutrient and carbon  
426 availability, and that phytoplankton respond more rapidly to these changes in nutrient  
427 concentrations than macrophytes themselves (Setaro & Melack, 1984; Mitchell, 1989; Eichel  
428 *et al.*, 2014). Importantly, however, the much larger reservoir of macrophytes biomass may

429 be able to repeatedly suppress these rapid increases in phytoplankton growth. Rooted  
430 macrophytes build up biomass over time and can also store nutrients (Faafeng & Mjelde,  
431 1998; Søndergaard & Moss, 1998; Yamamichi *et al.*, 2018), and thus probably prevented a  
432 high mean level of phytoplankton biomass and repeatedly suppressed multiple bouts of  
433 phytoplankton growth.

434 We implemented a model to explore how competitive interactions between  
435 macrophytes and phytoplankton might affect the mean vs. the variance of phytoplankton  
436 biomass. Specifically, we modelled competitive interactions such that macrophytes limit  
437 nutrient availability and phytoplankton limit light availability (Scheffer and Carpenter  
438 (2003)). This model reproduced the same contrast in phytoplankton biomass that we observed  
439 in the mesocosms: lower mean phytoplankton biomass but higher variance (CV) in the  
440 presence of macrophytes. Thus, the model predicted that phytoplankton biomass in a  
441 phytoplankton-dominated state would be more stable than in a macrophyte-dominated state  
442 under the same nutrient loading condition. At first sight, this result might appear  
443 counterintuitive as a macrophyte-dominated state is expected to be more stable to the  
444 unfavorable phytoplankton-dominated state. The biological explanation may be that when  
445 macrophytes and phytoplankton are competing for nutrients (and light), variation arising from  
446 the depletion of these resources is larger than with just one consumer (i.e. only phytoplankton  
447 in M-). However, whether variability is always expected to be higher in a macrophyte  
448 dominated than in a phytoplankton-dominated state, or under what conditions, would require  
449 more empirical work to validate. The model shows that this is the case when considering only  
450 one aspect of macrophyte-phytoplankton interactions (i.e. competition), which qualitatively  
451 matched with the high-resolution algal biomass data we collected. However, macrophytes can  
452 affect other compartments of the ecosystem (e.g. sediment, epiphytes, DOC) that are not  
453 considered in our model. For example, macrophytes can produce allelochemicals that inhibit

454 phytoplankton production (Hilt & Gross, 2008; Nakai *et al.*, 2012), modify the light  
455 environments via the production of DOC, or alter community structure of grazers; all of  
456 which could potentially influence the variance of phytoplankton biomass. Nevertheless, our  
457 study does illustrate that high resolution monitoring of ecosystem conditions (Mandal *et al.*,  
458 2019) and accompanying simulation models may provide new insights into the underlying  
459 mechanisms whereby macrophytes (or other foundation species) can affect ecosystem  
460 dynamics in general, and the relationships between mean and variance of ecosystem  
461 responses in particular.

462         In line with macrophytes being efficient primary producers in shallow lakes (Kaenel  
463 *et al.*, 2000), we confirmed our second hypothesis that mesocosm ecosystems with  
464 macrophytes had higher metabolic rates than those without macrophytes. Differences in  
465 productivity were most pronounced in July, where mesocosms with macrophytes were  
466 significantly more productive than macrophyte free mesocosms (t1). However, this difference  
467 disappeared during the phytoplankton bloom in the second measurement period (t2). This  
468 suggests that at intermediate concentrations, phytoplankton can increase productivity of  
469 aquatic ecosystems and match rates of primary production of macrophytes. Yet for any given  
470 chlorophyll-a biomass we measured, metabolic rates were higher when macrophytes were  
471 also present. This indicates that even at relatively low density, macrophytes (*Myriophyllum*,  
472 *Chara* and filamentous algae) can produce a significant metabolic signal. Higher productivity  
473 of ecosystems with macrophytes was also reflected in P:R ratio, which is on average slightly  
474 higher for those mesocosms in t3 and t4 (Sep 5th - Oct 9th). During t2 (Aug 7th - Aug 27th)  
475 there was a tendency for higher P:R in mesocosms without macrophytes, probably due to  
476 very high phytoplankton biomass. Towards the second half of the experiment, the growth of  
477 filamentous algae may have also contributed to higher rates of whole ecosystem productivity  
478 in +M tanks, where filamentous algae biomass was higher ( $8.33 \pm 10.54$  g dry weight, mean

479  $\pm$  SD) than in the -M tanks ( $3.21 \pm 5.46$  g dry weight, mean  $\pm$  SD). Overall, these findings  
480 suggest that macrophytes, regardless of their growth form, might make shallow lake  
481 ecosystems more productive across the seasonal succession of ecosystem metabolism  
482 (Madsen & Adams, 1988; Blindow *et al.*, 2006; Brothers *et al.*, 2013). These dynamics  
483 require additional investigation, especially in the context of successive phytoplankton blooms  
484 and their effects on the macrophyte community, but also in the context of rising temperatures  
485 and eutrophication.

486         Another important axis by which macrophytes affected the experimental ecosystems  
487 is their effects on the concentration and composition of dissolved organic matter. From the  
488 beginning of t2 (August 8<sup>th</sup>) to the end of the experiment (October 23<sup>rd</sup>), fDOM  
489 measurements in mesocosms with macrophytes were nearly twice as high as in mesocosms  
490 without macrophytes. Higher mean, but also lower variance of DOM was expected, because  
491 especially *Myriophyllum* is known to produce allelochemicals to inhibit algae growth that can  
492 persist in the water column (Hilt & Gross, 2008; Nakai *et al.*, 2012). However, total DOC  
493 concentrations were similar in both treatments, suggesting that not all components of the  
494 DOM-pool are affected the same way by macrophytes (Catalán *et al.*, 2014; Reitsema *et al.*,  
495 2018). Moreover, measurements from the scanning spectrophotometer showed consistently  
496 lower SSRs, indicating the presence of DOC compounds with higher molecular weight. The  
497 buildup and decay of macrophyte detritus could explain the low SSR ratios at similar total  
498 DOC levels, particularly since much of the initial *Chara* biomass contributed to  
499 decomposition rather than taking root, and/or grew but then decayed over the course of the  
500 experiment. However, *Myriophyllum* biomass also increased substantially, and could have  
501 added high MW compounds into the mesocosms. It is also possible that production rates of  
502 DOC were similar in M+ and M- treatments (as the total DOC was similar), but that material  
503 originating from macrophytes has a higher MW, and is more difficult to break down by

504 bacteria (Bolan *et al.*, 2011; Reitsema *et al.*, 2018). Overall, changes in DOC composition  
505 and variance might reflect differences in the balance of production and decomposition rates  
506 of different photosynthetic compounds, such as low MW sugars that are a byproduct of recent  
507 photosynthetic activity (Carpenter & Lodge, 1986; Bolan *et al.*, 2011; Reitsema *et al.*, 2018).  
508 However, more work needs to be done to understand the specific mechanisms behind such  
509 patterns, e.g. biomass production and decomposition or the production of secondary  
510 metabolites.

511         Using a common macrophyte assemblage, our experiment shows that communities of  
512 submerged plants can affect the mean and variance of a wide range of biotic and abiotic  
513 ecosystem properties and processes over a relatively short amount of time. Some of the  
514 effects we found on mean values, such as macrophytes decreasing phytoplankton biomass  
515 and increasing fDOM are not particularly surprising nor are they novel. However, the  
516 elevated variability of both phytoplankton pigments in the presence of macrophytes was  
517 unexpected, and potentially linked to competitive interactions. Across all our ecosystem  
518 metrics, we found that changes in CV covaried negatively with changes in the mean, or that  
519 CV increased despite no effect on the mean. Such results, show the importance of considering  
520 also the variance of ecological dynamics, which is increasingly recognized as an important  
521 aspect of ecosystem dynamics (Carpenter, 1988; Benedetti-Cecchi, 2003) and is used in a  
522 wide array of applications, e.g. ecological forecasting (Petchey *et al.*, 2015; Pennekamp *et al.*,  
523 2019), early warning signals for critical transitions (Scheffer *et al.*, 2009; Carpenter *et al.*,  
524 2011), and ecological modelling (Bartell *et al.*, 1988; Cottingham & Carpenter, 1998).  
525 Furthermore, our high frequency measurements can begin to reveal and quantify  
526 characteristic differences in timescales of ecosystem change, such as the high variability in  
527 phytoplankton communities vs. the relative stability of DOM and oxygen concentration  
528 throughout the season. Future experiments targeting shallow lake ecosystems should also

529 encompass measurements in high resolution, e.g. to detect the potential outcome of  
530 interactions among different trophic levels (e.g. between macrophytes, zooplankton and fish)  
531 or quantify the response to perturbations (e.g. nutrients or temperature). Our study highlights  
532 how complex and temporally variable interactions around foundation species can be and  
533 underscores the need for further research that investigates biotic and abiotic components of  
534 these networks of interactions in detail.

## 535 **Acknowledgements**

536 We thank Gilles Antoniazza, Emil Birnstiel, Laetitia Catalano, Daniel Steiner, Jaime M.  
537 Anaya-Rojas and Marek Svitok for major contributions to mesocosm set-up, maintenance,  
538 and sampling. Patrick Kathriner, and Beat Kienholz provided lab facilities and infrastructure  
539 support. The Eawag Directorate provided financial support for RJB. MDL was funded by the  
540 center for Adaptation to a changing Environment (ACE) at ETH Zürich

## 541 **Data Availability Statement**

542 Upon publication, all collected data will be made available via a data repository (Dryad).

## 543 **Conflict of interest**

544 The authors declare no conflict of interests.

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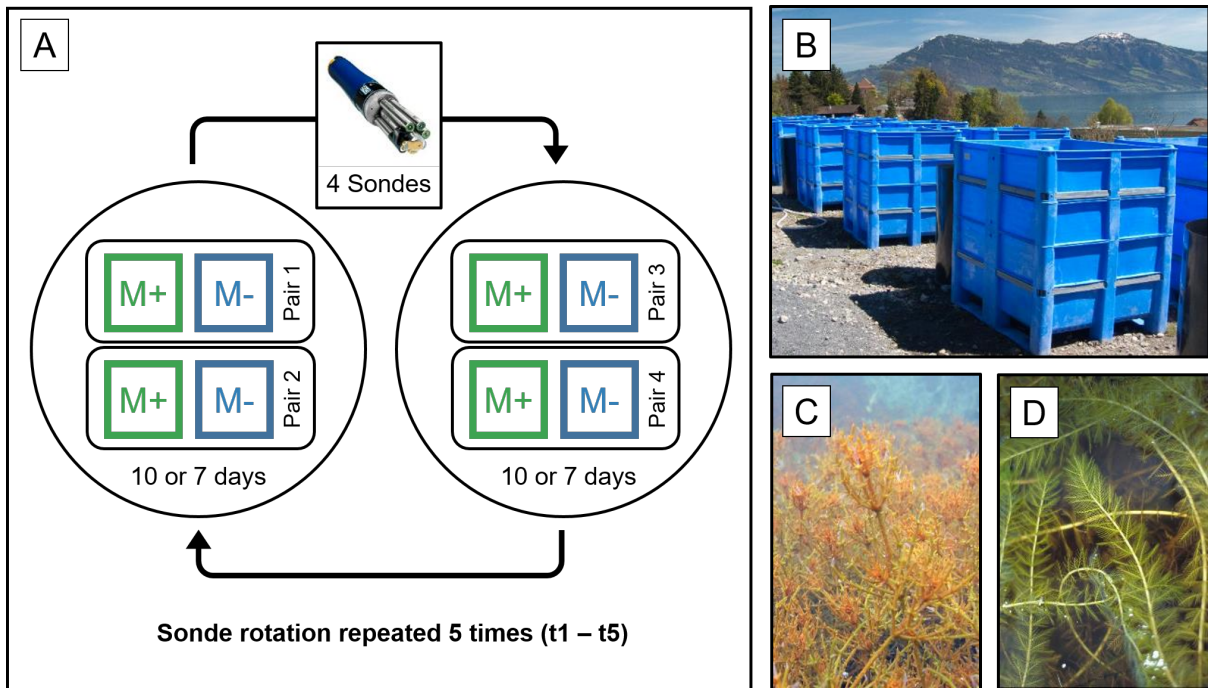
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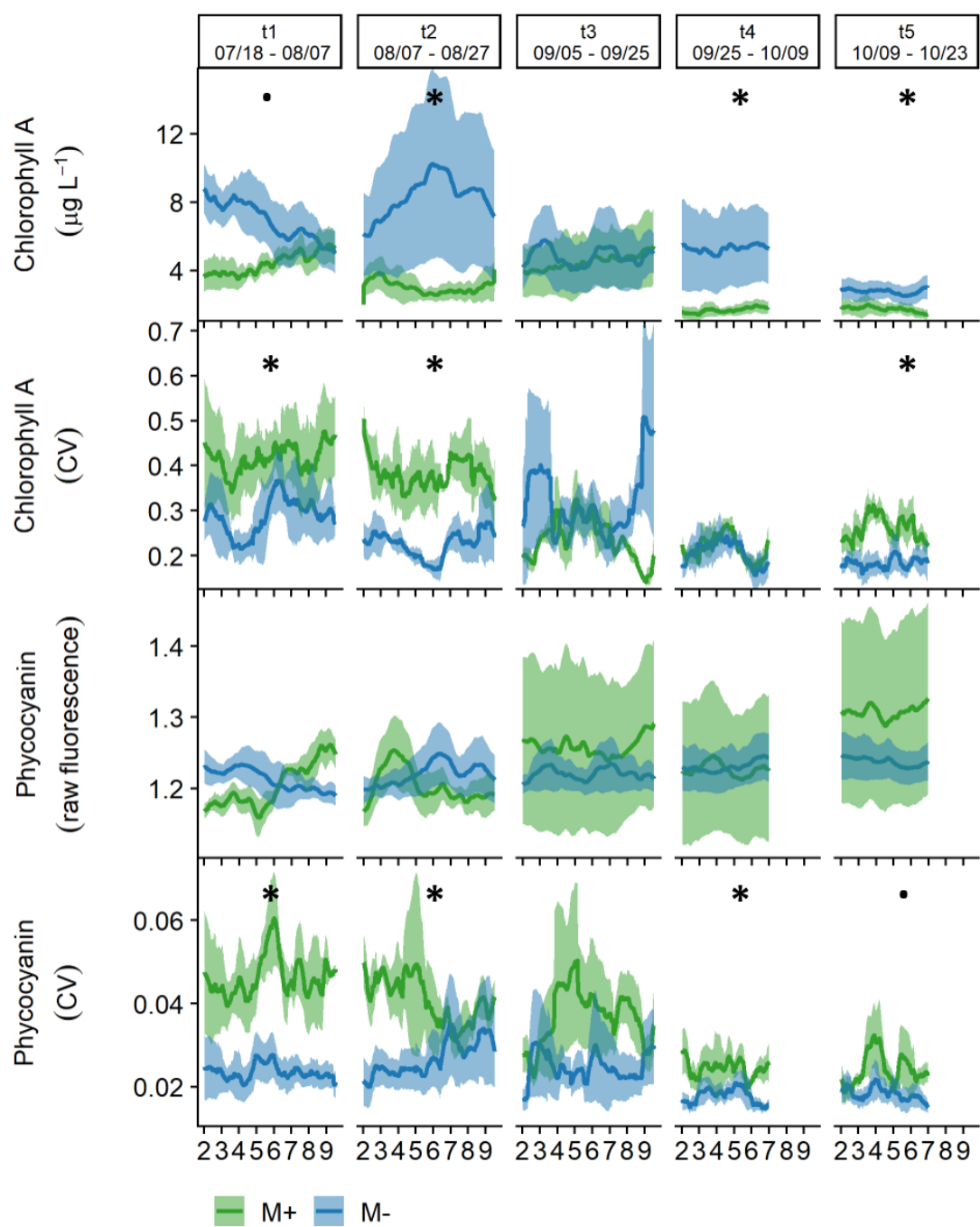




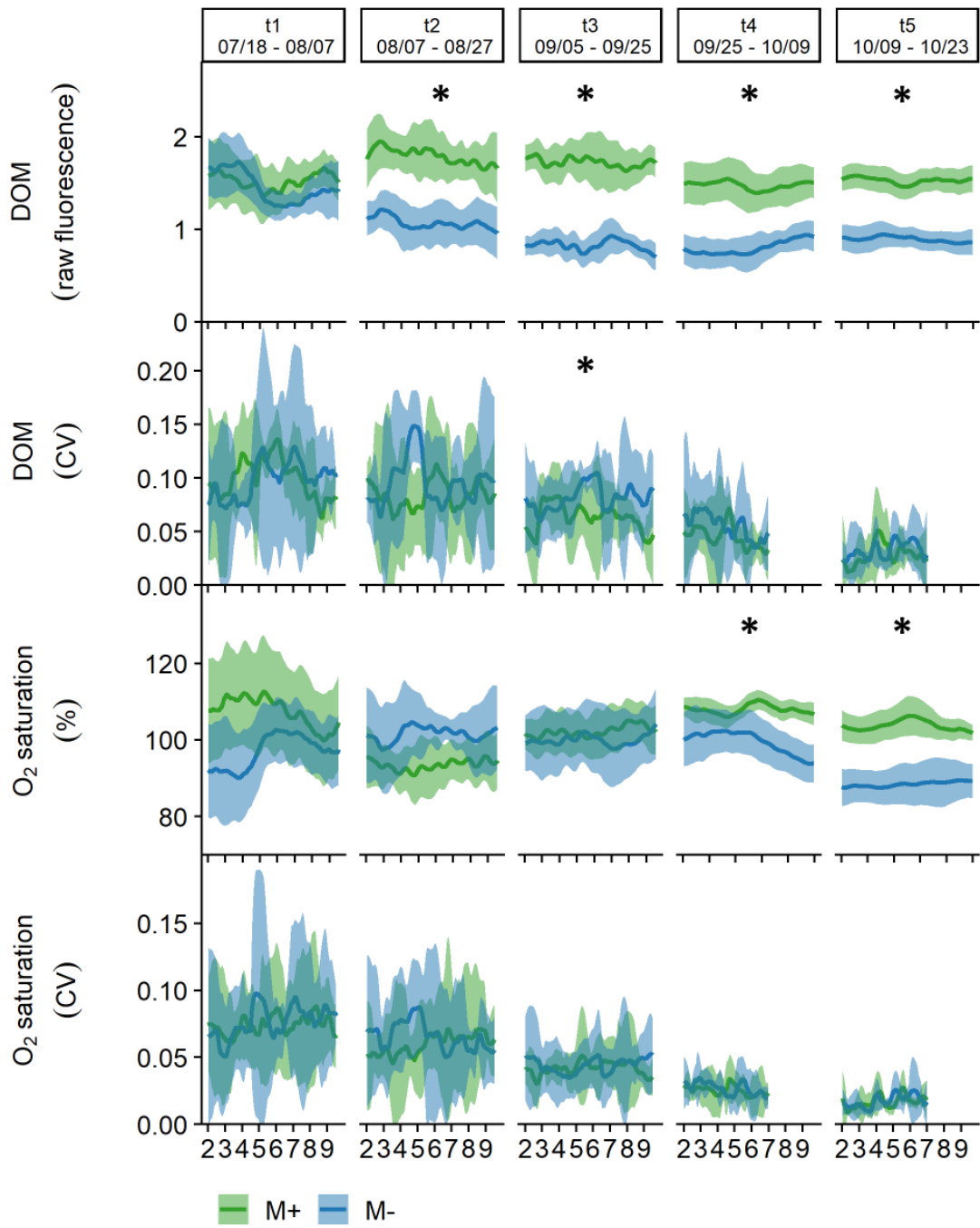
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750 1. A: Scheme of experimental procedure. Because we were limited to four sondes, we could  
 751 only measure two tank pairs of macrophyte (M+)/no macrophyte (M-) contrasts. To measure  
 752 all eight tanks, we followed a rotation scheme in which every tank was measured for 10  
 753 consecutive days before the sondes were moved to another tank (for details refer to Methods  
 754 section). B: Picture of experimental site showing the set up mesocosms (1000L). C: *Chara*  
 755 *tomentosa* (Photo credit: Gustav Johansson). D: *Myriophyllum spicatum* (Photo credit: Alison  
 756 Fox).

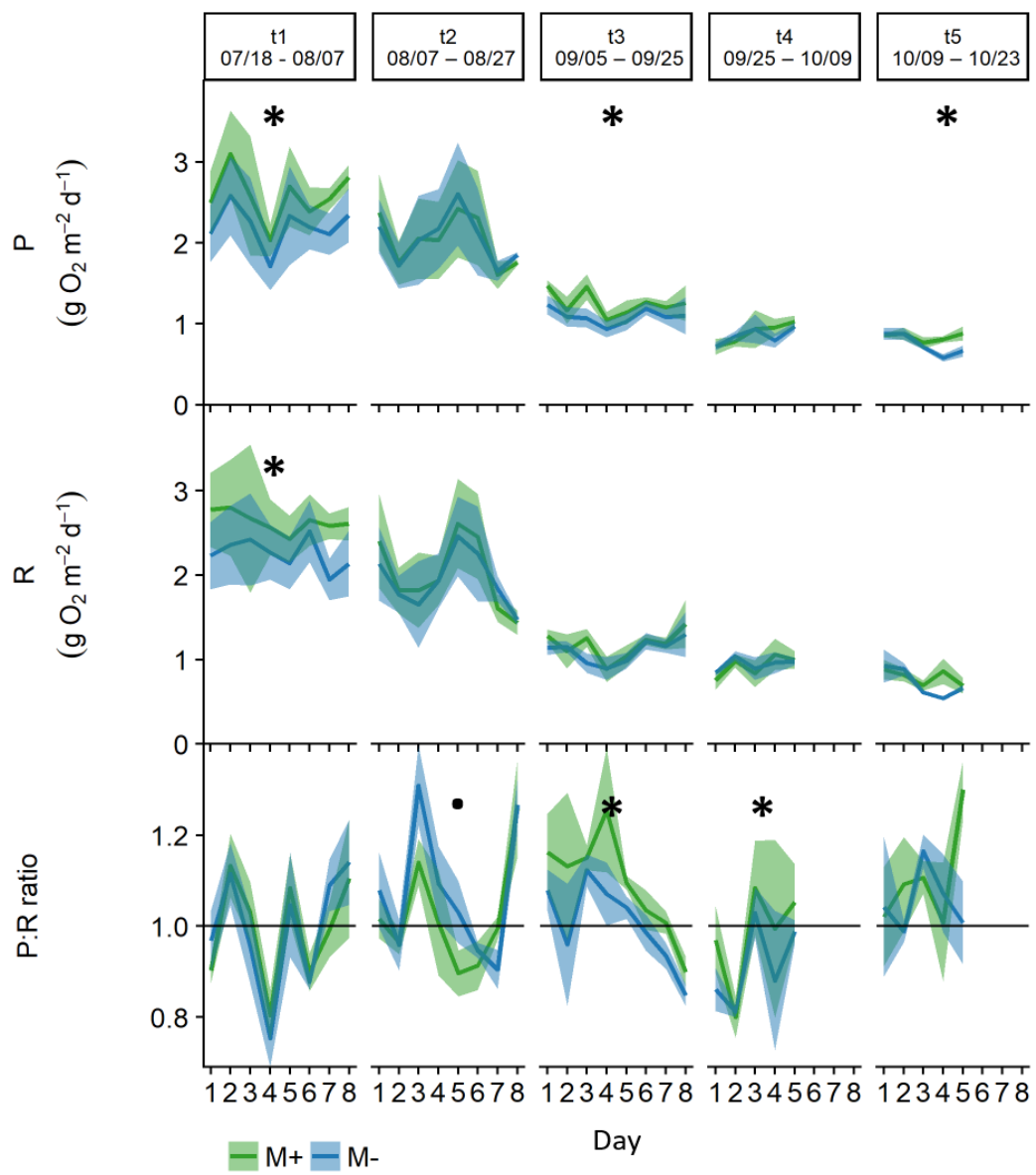
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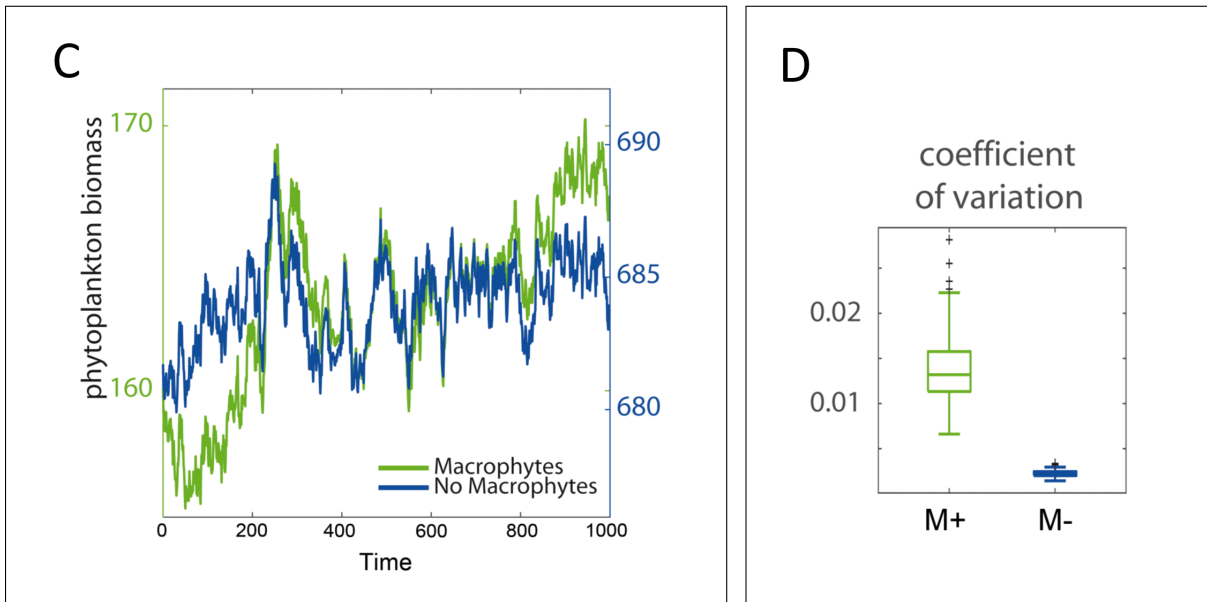
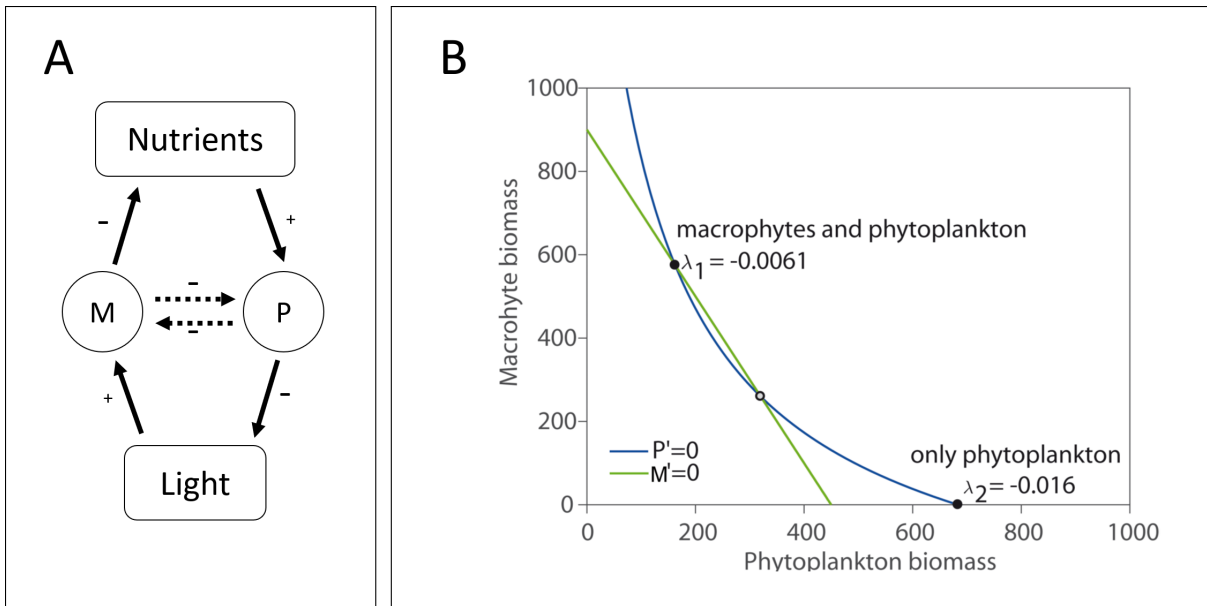
759 2. Sliding window results from high frequency measurements of chlorophyll-a and  
760 Phycocyanin over time (days 2-9 in each of five consecutive sampling periods). Lines show  
761 Mean  $\pm$  SE (n = 8 tanks), asterisks indicate significant differences ( $p \leq 0.05$ ), dots indicate  
762 marginal significance ( $p \leq 0.1$ ). One GAM was used per period, including tank and the pair  
763 it was in (see Fig.1) as random effects. Here the sliding window time series of the Mean from  
764 both blocks are shown pooled for better illustration. Because the sliding window had a width  
765 of one day, only aggregate days 2-9 for each measurement are shown.



767 3. Sliding window results from high frequency measurements of fDOM and dissolved oxygen  
768 over time (days 2-9 in each of five consecutive sampling periods). Lines show Mean  $\pm$  SE (n  
769 = 8 tanks), asterisks indicate significant differences ( $p \leq 0.05$ ). One GAM was used per  
770 period, including tank and the pair it was in (see Fig.1) as random effects. Here the sliding  
771 window time series of the Mean from both blocks are shown pooled for better illustration.  
772 Because the sliding window had a width of one day, only aggregate days 2-9 for each  
773 measurement are shown.



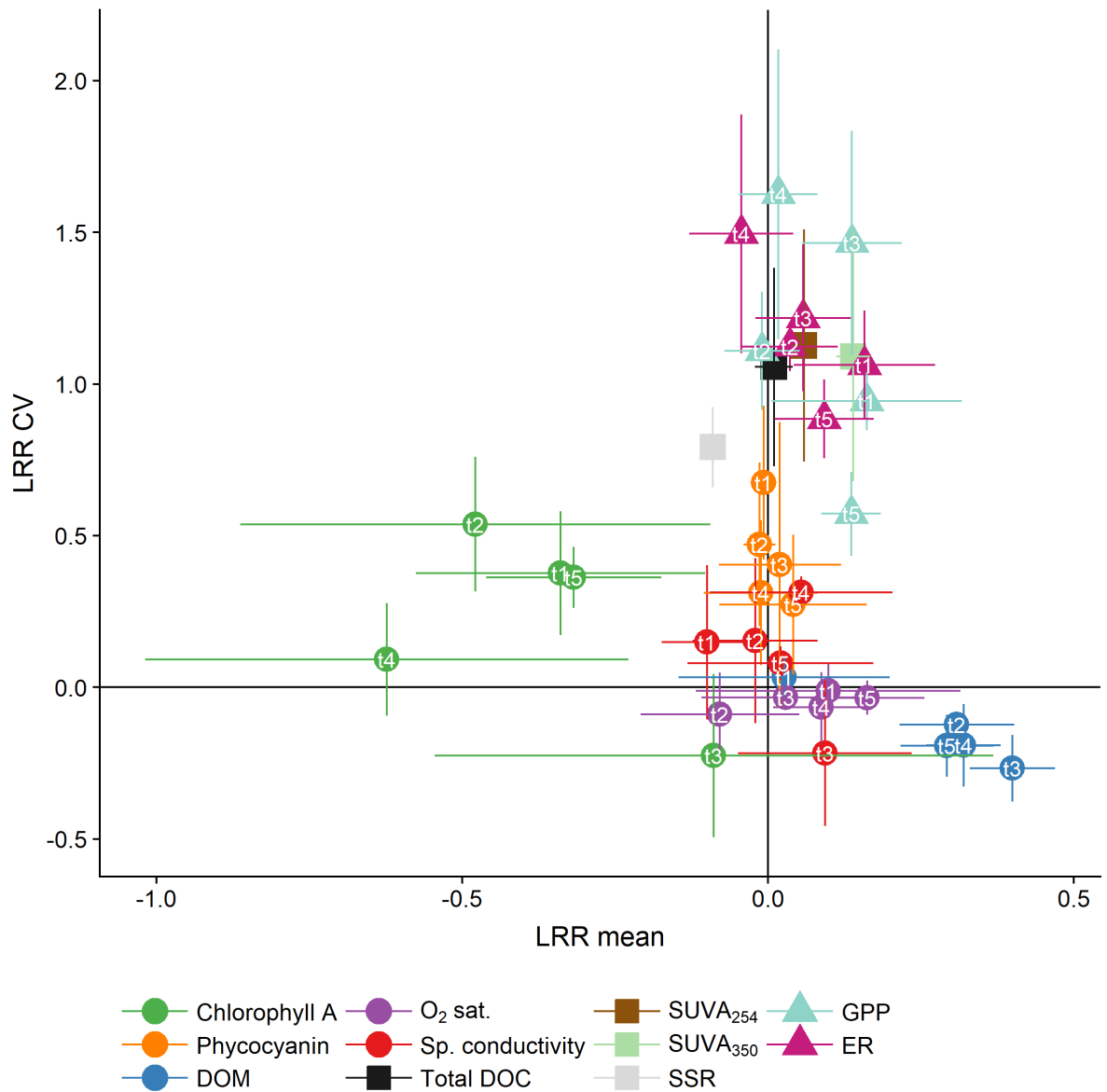
775 4. Ecosystem productivity (P), respiration (R) and P:R ratio calculated from high frequency  
776 measurements of O<sub>2</sub> saturation, temperature, light, and air pressure. Shown are Mean ± SE  
777 (n= 8 tanks), asterisks indicate significant differences, dots indicate marginal significance (p  
778 ≤ 0.1). One GAM was used per period, including both consecutive blocks as random  
779 variables. Here the time series of metabolic rates from both blocks are shown pooled for  
780 better illustration. The modelling procedure requires full days to be included, but because of  
781 the model parameterization to start each day 1 hour before sunrise, the last day is incomplete  
782 and thus cannot be modeled. Hence, only aggregate days 1-8 are shown.  
783





786 5. A simple model of competition for light and nutrients between macrophytes and  
787 phytoplankton (for details see Supplement). A: Schematic of interactions between  
788 macrophytes (M) and phytoplankton (P). Macrophytes consume nutrients, which has a  
789 negative indirect effect on phytoplankton. If phytoplankton biomass becomes too high, it  
790 reduces light levels such that there is a negative indirect effect on macrophytes. Thus,  
791 macrophytes are more strongly limited by light, and phytoplankton by nutrients. B: Zero-  
792 growth curves of macrophytes (green line) and phytoplankton (blue line). Black points mark  
793 the 2 alternative stable equilibria of either a macrophyte-and-phytoplankton state or an only-  
794 phytoplankton state. Although these two states exist for the same level of nutrients in the  
795 water, their stability (measured as the dominant eigenvalue  $\lambda$ ) differs: the only-  
796 phytoplankton is more stable than the macrophyte-and-phytoplankton state. C: Simulated  
797 time series of phytoplankton biomass in the presence (green) and in the absence (blue – note  
798 second y-axis) of macrophytes for the same level of nutrients in the water. D: Coefficient of  
799 variation of phytoplankton biomass estimated from 200 simulated sets.

800



802

803 6. Average log response ratios (LRR) for macrophyte presence on mean and CV. Effect sizes  
 804 were calculated differently for each data type: high frequency (●), metabolism (▲), or DOC  
 805 point measurements (■) – for details refer to the methods section. Each point shows the  
 806 average (mean ± se) macrophyte LRR across all tank pairs (N=4, Fig. 1) and in all  
 807 measurement periods (t1-t5, except for the DOC point measurements, where all 10  
 808 measurements were used to calculate LRR for mean and CV).

## 809 **Tables**

810 1. Parameters measured in high frequency using autonomous sondes. Prior to the experiment  
811 we performed a cross-comparison trial with all four sondes, after which we corrected all  
812 sensors for relative differences among them (i.e., “cross” = calibrated against each other).  
813 Chlorophyll-a sensors were additionally calibrated with samples taken during this trial that  
814 were analyzed for their chlorophyll-a content with high pressure liquid chromatography  
815 (HPLC). Oxygen sensors were calibrated against water-saturated air. (\*fDOM-sensors  
816 measure emission at  $365\pm 5$  and excitation at  $480\pm 40$  nm. \*\*For metabolism modelling mg/L  
817 output was used.)

Parameter	Unit	Sensor type	Calibration
Chlorophyll A	mg/L	Optical, fluorescence	HPLC, cross
Phycocyanin	Raw fluorescence	Optical, fluorescence	cross
fDOM	Raw fluorescence	Optical, fluorescence *	cross
Dissolved oxygen	% saturation**	Optical, luminescence	Saturated air, cross
Conductivity	$\mu\text{S}/\text{cm}$	4-electrode cell	Conductivity standard
Temperature	$^{\circ}\text{C}$	Thermistor	cross

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819

820 2. Statistical results of GAM-models testing time series of water parameters and metabolic  
821 rates. Results are from individual models (one model per parameter and measurement  
822 period). For mean and CV of water parameters, N per model is 768 for t1-t3 and 480 for t4  
823 and t5. For metabolic rates, N per model is 8 23for t1-t3 and 5 for t4 and t5. Trends (p<0.1)  
824 indicated by bold font, significant results (p<0.05) indicated by underlined bold font. t-value  
825 = model estimate / model estimate SD, Rsq = R squared of model fit.

826

	t1			t2			t3			t4			t5		
Mean	t-value	p-value	Rsq	t-value	p-value	Rsq	t-value	p-value	Rsq	t-value	p-value	Rsq	t-value	p-value	Rsq
Chlorophyll A	1.724	<b>0.085</b>	0.809	2.6961	<b>0.007</b>	0.945	0.555	0.722	0.863	3.140	<b>0.001</b>	0.916	3.600	<b>&lt;0.001</b>	0.927
Phycocyanin	0.311	0.756	0.748	0.637	0.524	0.752	-0.445	0.656	0.865	0.006	0.995	0.883	-0.727	0.467	0.875
fDOM	-0.302	0.762	0.641	-4.923	<b>&lt;0.001</b>	0.889	-9.620	<b>&lt;0.001</b>	0.963	-6.690	<b>&lt;0.001</b>	0.983	-6.553	<b>&lt;0.001</b>	0.966
Dissolved oxygen	-0.877	0.380	0.758	1.163	0.245	0.779	-0.350	0.726	0.816	-2.013	<b>0.044</b>	0.856	-3.265	<b>0.001</b>	0.892
Temperature	-0.082	0.934	0.448	0.386	0.699	0.734	-0.370	0.711	0.646	0.657	0.511	0.775	-0.113	0.910	0.901
Conductivity	2.064	<b>0.039</b>	0.968	0.112	0.911	0.939	-1.165	0.244	0.907	-0.533	0.594	0.875	-0.019	0.985	0.884
CV	t-value	p-value	Rsq	t-value	p-value	Rsq	t-value	p-value	Rsq	t-value	p-value	Rsq	t-value	p-value	Rsq
Chlorophyll A	-2.041	<b>0.041</b>	0.784	-3.310	<b>0.001</b>	0.799	1.578	0.115	0.551	-0.388	0.698	0.661	-2.803	<b>0.005</b>	0.734
Phycocyanin	-4.846	<b>&lt;0.001</b>	0.668	-2.092	<b>0.037</b>	0.557	-1.354	0.176	0.621	-2.105	<b>0.035</b>	0.541	-1.886	<b>0.059</b>	0.696
fDOM	-0.052	0.958	0.508	1.119	0.263	0.357	4.036	<b>&lt;0.001</b>	0.426	0.746	0.456	0.629	0.431	0.666	0.492
Dissolved oxygen	0.244	0.808	0.617	1.186	0.236	0.558	0.949	0.343	0.319	0.566	0.571	0.363	0.312	0.755	0.404
Temperature	-0.233	0.816	0.324	-0.253	0.801	0.446	0.914	0.361	0.257	0.193	0.847	0.415	0.886	0.376	0.430
Conductivity	-0.278	0.781	0.339	-0.966	0.334	0.358	1.664	<b>0.096</b>	0.374	-0.989	0.323	0.464	-0.062	0.950	0.583
Metabolism	t-value	p-value	Rsq	t-value	p-value	Rsq	t-value	p-value	Rsq	t-value	p-value	Rsq	t-value	p-value	Rsq
P	-3.653	<b>&lt;0.001</b>	0.705	-1.165	0.249	0.461	-2.147	<b>0.036</b>	0.169	1.381	0.176	0.046	-3.395	<b>0.002</b>	0.406
R	-3.470	<b>0.001</b>	0.329	0.121	0.905	0.545	-0.367	0.360	0.456	-0.415	0.681	0.235	-0.346	0.340	0.230
PR	0.160	0.874	-0.033	1.816	<b>0.074</b>	-0.005	-4.812	<b>&lt;0.001</b>	0.090	-3.389	<b>0.002</b>	0.303	-0.650	0.520	0.119

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