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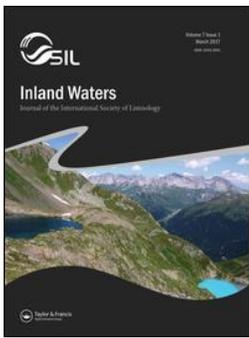
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Macrophyte species strongly affects changes in C, N, and P stocks in shallow lakes after a regime shift from macrophyte to phytoplankton dominance

Hai Jun Wang,^{1*} Hong Zhu Wang,¹ Xiao Min Liang,¹ Bao Zhu Pan,^{1,2} and Sarian Kosten³

¹State Key Laboratory of Freshwater Ecology and Biotechnology, Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan, China

²Changjiang River Scientific Research Institute, Wuhan, China

³Department of Aquatic Ecology and Environmental Biology, Institute of Water and Wetland Research, Radboud University Nijmegen, Nijmegen, The Netherlands

*Corresponding author: wanghj@ihb.ac.cn

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Abstract

Shallow lakes are important stocks of carbon (C), nitrogen (N), and phosphorus (P), yet little is known about the influence of alternative primary producer dominance on C stocks or the impact of different macrophyte species on the role of shallow lakes as elemental stocks. We used Yangtze shallow lakes dominated by a monsoon climate as a research site to test the hypothesis that changes in elemental stocks in the water column and sediment after a shift to a phytoplankton-dominated state depend on the macrophyte species originally present. We used a dual approach, combining multi-year monitoring and multi-lake comparisons of lakes that were, at least once, dominated either by fast-decomposing *Potamogeton crispus* or slow-decomposing *P. maackianus*. Elemental concentrations generally decreased in the water column and increased in sediment after a shift from *P. maackianus* presence to absence. Only a minor reallocation of elemental stocks was found in lakes where *P. crispus* disappeared. This difference is likely caused by a combination of the different biomass and decomposition rates between species, further illustrated by the amount of dead plant material in the sediment after loss of plants. After *P. maackianus* loss, plant material was found in the sediment in high amounts for up to 6 years, whereas after *P. crispus* loss the coarse material was absent in <1 year. Suspended and dissolved concentrations (i.e., the mobile pool) of C increased 1.5–1.9-fold and P increased 2.0–4.3-fold after the shift, whereas N tended to decrease or stay unchanged. Higher mobile pools of C and P after macrophytes loss implies a more vulnerable watershed, supporting higher phytoplankton biomass in the lakes and causing serious downstream eutrophication problems.

Key words: alternative states, decomposition rates, elemental stocks, *Potamogeton crispus*, *P. maackianus*, shallow lakes

Introduction

Lakes are widely recognized as important stocks of carbon (C; Dean and Gorham 1998, Kortelainen et al. 2004), nitrogen (N; Saunders and Kalff 2001), and phosphorus (P; Carpenter et al. 1992, Spears et al. 2007), and interest in factors influencing amounts of C, N, and P sequestered and

stored in lakes has grown. Small shallow lakes, forming the majority of world lakes (Downing et al. 2006), store disproportionately high amounts of C (Dong et al. 2012, Anderson et al. 2014). Their relatively small size and limited depth directly influences the way they function as C, N, and P stocks. The water residence time in shallow lakes is generally short (an order of magnitude of months to a year; Peters and Lodge 2010), implying short-term

storage of elements in the water. Burial in the sediment, however, leads to long-term storage (decades to centuries). Elemental stocks vary greatly among systems (Tranvik et al. 2009) and are influenced by watershed characteristics (Sobek et al. 2003, Heathcote and Downing 2012) and climate, for instance with a reduced C storage under warmer conditions (Gudasz et al. 2010, Kosten et al. 2010).

The type of primary producers dominating a system likely affects the elemental storage as well because of their effects on the elemental exchange (generally strong in shallow lakes) between water and sediment (Peters and Lodge 2010). Fundamental differences in P allocation between water and sediment exist, for instance, between phytoplankton and rooted macrophyte-dominated systems. Growth of phytoplankton relies on nutrients in water and can mobilize P to some extent through the creation of anoxic conditions at the sediment surface (Scheffer 1998). Macrophytes can, however, mobilize high amounts of elements from the sediment through root uptake (Barko 1981). Shifts in primary producer dominance are also known to influence N stocks through alteration of denitrification rates (Piña-Ochoa and Álvarez-Cobelas 2006). Ultimately, elemental stocks are influenced by decomposition rates after die-off. Phytoplankton tend to have faster decomposition rates than macrophytes, although large variability in decomposition rates exists within life forms of macrophytes (Enriquez et al. 1993). Submersed macrophytes tend to have the fastest decomposition rates, followed by floating-leaved and emergent macrophytes (Enriquez et al. 1993, Chimney and Pietro 2006).

To date, the effect of a shift from macrophyte to phytoplankton dominance on elemental stocks has focused mainly on P and N (Scheffer 1998, Piña-Ochoa and

Álvarez-Cobelas 2006). The effect of shifts in primary producers on C stocks is less well known (but see Brothers et al. 2013, who found higher C burial during phytoplankton dominance), although shallow lakes have been recognized as C burial hot spots (Brezonik and Engstrom 1998, Moreira-Turcq et al. 2004, Gui et al. 2013). Here we hypothesize that shifts from macrophyte presence to absence not only strongly affect the functioning of lakes as P and N stocks by reallocating elements from the water column to sediment and vice versa, but for C as well (hypothesis 1). Clearly, large variations exist between different macrophyte species as well, for example regarding their biomass and decomposition rates. Decomposition rates of submersed macrophytes, for instance, vary an order of magnitude among species (Chimney and Pietro 2006). In a lake losing its slowly decomposing macrophytes, sediment stocks might increase to a greater extent and for a longer time period than in a lake with a die-off of rapidly decomposing macrophytes (hypothesis 2).

We tested these hypotheses using data from 8 lakes in the mid-lower Yangtze Basin, located in the monsoon subtropics, comprising numerous shallow lakes (>800 lakes >1 km²; Ma et al. 2011). These lakes act as substantial regional C sinks (Dong et al. 2012) because of their large total area (15770 km²) and considerable variation in burial rate of C, ranging from <5 to >300 g m⁻² yr⁻¹ (Dong et al. 2012). Little is known, however, about what drives the C burial in sediments of Yangtze floodplain lakes. In this basin, shifts between the contrasting states have been found to widely occur in shallow lakes (Wang et al. 2014); therefore, we must consider how these changes will influence the patterns of C, N, and P transport in watersheds.

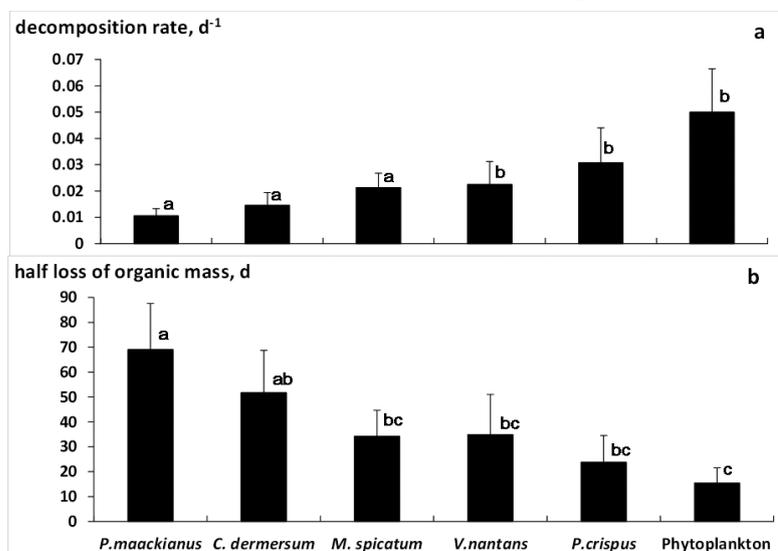


Fig. 1. (a) Decomposition rates and (b) half loss of organic mass (mean and standard deviation) of submersed macrophyte species commonly found in the mid-lower Yangtze lakes (*P. Potamogeton*, *C. Ceratophyllum*, *M. Myriophyllum*, *V. Vallisneria*) and of phytoplankton. Different letters indicate significant differences (see Appendix for references).

In the mid-lower Yangtze Basin, the most common submersed macrophytes are *Ceratophyllum demersum*, *Myriophyllum spicatum*, *Potamogeton crispus*, *P. maackianus*, and *Vallisneria spiralis*. To test our hypotheses, we focused on lakes dominated by either *P. crispus* or *P. maackianus*, macrophytes with the highest and the lowest decomposition rates, respectively (Fig. 1). We used 2 approaches: (1) we compared C, N, and P stocks in lakes before and after a shift from being dominated by either *P. crispus* or *P. maackianus* to phytoplankton-dominated during a period of 9 years; and (2) we compared C, N, and P stocks in 18 lakes dominated for at least one growing season by either *P. crispus* or *P. maackianus*.

Study site

All the lakes studied are located in the mid-lower Yangtze Basin (29°38'–31°30'N; 113°11'–120°51'E), dominated by a warm humid subtropical monsoon climate. The annual mean air temperature ranges between 14 and 18 °C and precipitation between 1000 and 400 mm. All are shallow floodplain lakes, isolated from the Yangtze River by embankments and sluice gates, with altitudes generally <50 m a.s.l.

Our study included 8 systems (Fig. 2 and Table 1). Lake Bao'anhu was divided into 13 subareas with nets or dikes, of which 11 subareas were included in this study. One-way ANOVA analyses by Wang et al. (2005) indicated significant differences in environmental variables (e.g., nutrient levels and transparency) among subareas. Water exchange between the subareas, if any, can be neglected. We therefore, treated these subareas as individual lakes, leading to 18 study lakes.

Methods

Sampling and measurements

The lakes were sampled every season during 2003–2012. The number of sites where water samples were taken each time in each lake ranged from 3 to 12, depending on lake size. For each site, water samples were taken at 0.5 m below the surface and at half water depth and mixed for measurement. Water depth (Z), Secchi depth (Z_{SD}), and submersed macrophyte biomass (B_{Mac}) were further measured between these water sample sites to capture more of the spatial variability of the lake, resulting in 5–23 sampling sites of Z , Z_{SD} , and B_{Mac} in each lake. The analyses were based on the averages of these sites for each lake. Analyses for total nitrogen (TN) and phosphorus (TP) of lake water and phytoplankton chlorophyll *a* (Chl-*a*) followed the Chinese Water Analysis Methods Standards (Huang et al. 1999). TN was measured by the alkaline potassium persulfate digestion-UV spectrophotometric method; TP by the ammonium molybdate-ultraviolet spectrophotometric method; Chl-*a* after acetone extraction by reading absorbance at 665 and 750 nm using a spectrophotometer (Unico UV-2000, Shanghai, China); and Z and Z_{SD} by a sounding lead and a Secchi disk, respectively.

The diversity and biomass of submersed macrophytes were measured by random sampling (2–4 replicates) at each site using a scythe-type sampler (sampling area 0.2 m²) with a long handle. Generally, 3 replicates were taken; only 2 were taken in cases of extremely abundant macrophytes with low variability in density, and 4 were taken in cases of scarce macrophytes and high variation in

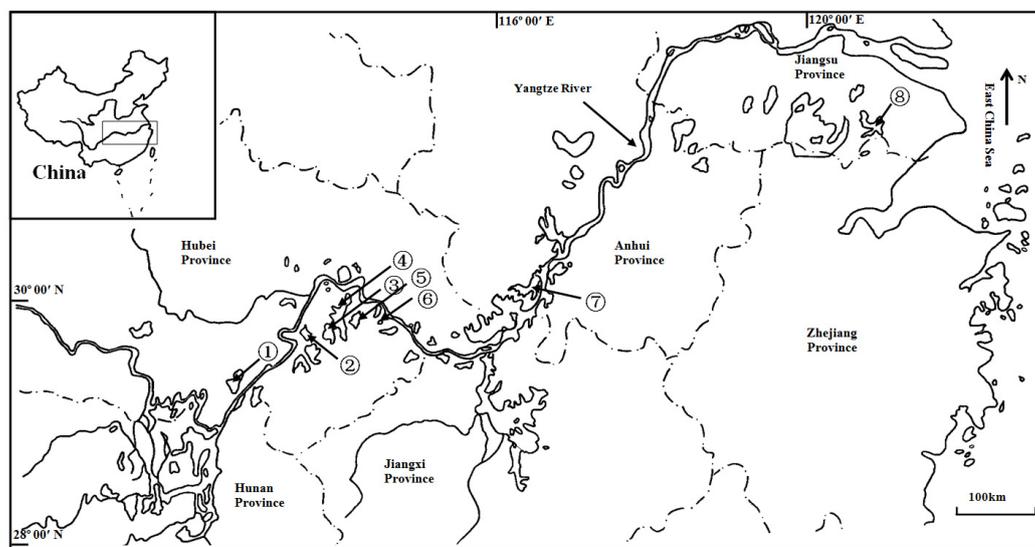


Fig. 2. Distribution of the lakes studied along the Yangtze River. ① Lake Honghu; ② Lake Luhu; ③ Lake Ninggang; ④ Lake Niushanhu; ⑤ Lake Bao'anhu (including 11 subareas); ⑥ Lake Huamahu; ⑦ Lake Wuchanghu; and ⑧ Lake Yangchenghu.

Table 1. Basic morphological data of the lakes studied, with the years and number of months investigated and the alternative stable states.

Lakes	Surface area, km ²	Mean depth, m	Investigation years	Number of lake-months	Alternative states
Honghu	355	1.35	2003, 2004, 2008	3	<i>Potamogeton maackianus</i> (P.m.) present
Niushanhu	38.0	2.50	2003, 2005, 2007, 2008	5	
Ninggang	9.7	1.80	2008	1	
Luhu	29.8	2.20	2005, 2008	2	<i>P. crispus</i> (P.c.) present
Huamahu	10.3	1.80	2003, 2004	2	
Wuchanghu	88.5	1.80	2004	1	
Yangchenghu	113.0	1.43	2004	1	
Bao'ankou*	3.6	2.18	2005–2012	17	Cyclic shifts between P.c. present and absent
Huangfengkou*	1.9	1.93	2006, 2010–2012	9	
Yexizui*	4.7	2.42	2006, 2010–2012	8	
Zhuzhou*	6.5	2.55	2010–2012	7	
Changlingzhou*	8.8	2.50	2010–2012	6	
Longwangtou*	6.3	2.54	2010–2012	7	
Lianhuazhou*	1.6	2.64	2009–2012	11	Shifted from P.m. present to absent in early May, 2002
Tongshawan*	1.9	2.21	2009–2012	9	late July, 2002
Outang*	1.5	2.53	2008–2012	9	late October, 2002
Shuimiao*	1.6	2.33	2004–2012	21	late October, 2006
Changlingtou*	1.5	1.86	2004–2012	21	late October, 2006

* Subareas of Lake Bao'anhu

density. As a result, the total sampling area for a specific lake ranged mostly between 4 and 12 m², depending on lake size and density of macrophytes. Samples were then combined, cleaned (removal of extraneous material such as sticks, macroinvertebrates, and substrates), blotted dry, and weighed for wet biomass.

Sediment samples were taken with a core sampler (90 mm diameter) at 1–3 sites in each lake. The top 10 cm of the sediment was air-dried and subsequently ground to pass through a 149 µm sieve. The concentrations of organic matter (OM_{Sed}), total nitrogen (TN_{Sed}), and total phosphorus (TP_{Sed}) were then determined by wet oxidation in the presence of excess dichromate and subsequent spectrophotometry (OM_{Sed}); the Kjeldahl method and titrimetry (TN_{Sed}); and dry mineralization using sulphuric-perchloric acid and spectrophotometry using molybdenum blue (TP_{Sed}; Bao 2000, Golterman 2004).

Coarse detritus was collected from sediment sampled with a Peterson sampler (1/16 m²) and cleaned gently with a 6.4 µm sieve. In the laboratory, macroinvertebrates and large pieces of terrestrial plant residues were separated by hand. Water was added to sandy sediment to float the detritus, and the water with the detritus was

then passed over another sieve of the same size. The detritus was collected and air-dried in glass culture dish, then oven-dried for 1 h at 105 °C and weighed to 0.01 g.

Three lakes were dominated by *P. maackianus* during the entire study period, and in 5 lakes, shifts from *P. maackianus* presence to absence occurred. These lakes are further referred to as *P. maackianus* lakes. Four lakes were dominated by *P. crispus* during the entire study period, whereas 6 other lakes shifted cyclically between *P. crispus* presence and absence (further referred to as *P. crispus* lakes). In total, a dataset of 140 lake-months was obtained. A subset of 60 lake-months was obtained for *P. crispus* lakes: 20 lake-months of macrophyte-presence and 40 lake-months of macrophyte-absence. For *P. maackianus* lakes, a subset of 80 lake-months was obtained: 26 lake-months with macrophyte-presence and 54 lake-months with macrophyte-absence. For multi-year comparison, 59 lake-months from 3 lakes (i.e., Bao'ankou supporting *P. crispus*, Shuimiao and Changlingtou supporting *P. maackianus*) during 2004 to 2012 were included. For multi-lake comparison, 81 lake-months were included.

Calculation and analyses

The concentrations of C, N, and P in the sediment were expressed as g m^{-2} to compare with the water column content:

$$C_{\text{Sed}} = \rho_{\text{Sed}} (1000 \text{ kg m}^{-3}) \times \text{OC}_{\text{Sed}} (\text{g kg}^{-1}) \times 0.1 \text{ m}, \quad (1)$$

and

$$N_{\text{Sed}} (\text{or } P_{\text{Sed}}) = \rho_{\text{Sed}} (1000 \text{ kg m}^{-3}) \times \text{TN}_{\text{Sed}} (\text{or } \text{TP}_{\text{Sed}}) (\text{g kg}^{-1}) \times 0.1 \text{ m}, \quad (2)$$

where ρ_{Sed} is the density of dried sediment calculated from an empirical equation obtained by Menounos (1997):

$$\rho_{\text{Sed}} = \ln(0.303 \times [\text{OM } \%]^{0.39}) / (-0.97), \quad (3)$$

where OC_{Sed} is organic carbon concentration in sediment calculated as $0.40 \text{ OM}_{\text{Sed}}$ (Reddy and Declaune 2008).

To explore how the shifts from macrophyte presence to absence reallocate elements in the water column, phytoplankton and macrophytes were separated from water when analysing concentrations of elements. The elemental pool in the water column ($C/N/P_{\text{WaterColumn}}$) therefore consisted of 3 components: water ($C/N/P_{\text{Water}}$), phytoplankton ($C/N/P_{\text{Algae}}$), and macrophytes ($C/N/P_{\text{Mac}}$).

The concentrations of elements in water column were calculated as:

$$C_{\text{WaterColumn}} = (\text{TOC} + \text{DIC}) (\text{g m}^{-3}) \times Z (\text{m}) + C_{\text{Mac}} (\text{g m}^{-2}), \quad (4)$$

and

$$N_{\text{WaterColumn}} (\text{or } P_{\text{WaterColumn}}) = \text{TN} (\text{or } \text{TP}) (\text{g m}^{-3}) \times Z (\text{m}) + N_{\text{Mac}} (\text{or } P_{\text{Mac}}) (\text{g m}^{-2}). \quad (5)$$

The sum of total organic C and dissolved inorganic C of lake water ($\text{TOC} + \text{DIC}$) represents the dissolved and particulate C in the water column (including phytoplankton; equation 6); TN and TP reflect the N and P concentrations in the water column; and C_{Mac} , N_{Mac} , and P_{Mac} are the concentrations of C, N, and P incorporated in living macrophytes (equation 7).

The sum of TOC and DIC was calculated from an empirical regression equation ($R^2 = 0.76$, $n = 22$,

$p < 0.001$), reanalysed from Xing (2007) based on lakes from the same region:

$$\text{TOC} + \text{DIC} = 0.21 \text{ Chl-}a + 15.35. \quad (6)$$

C_{Mac} , N_{Mac} , and P_{Mac} were calculated as:

$$C_{\text{Mac}} (\text{or } N_{\text{Mac}}, P_{\text{Mac}}) (\text{g m}^{-2}) = B_{\text{Mac}} \text{DW} \times C\%_{\text{Mac}} (\text{or } N\%_{\text{Mac}}, P\%_{\text{Mac}}), \quad (7)$$

where $B_{\text{Mac}} \text{DW}$ is dry biomass of submersed macrophytes calculated by multiplying the wet biomass by 0.08 (i.e., the average percentage conversion factor for submersed macrophytes; Chen and Ho 1975). The percentages of biomass comprising the different elements ($C\%_{\text{Mac}}$, $N\%_{\text{Mac}}$, and $P\%_{\text{Mac}}$) were derived from literature (Appendix Table S1). For *P. crispus*, the average percentages were 34.6%, 3.07%, and 0.39%, respectively, and for *P. maackianus* were 38.1%, 3.28%, and 0.17%.

The concentrations of elements in water are hence calculated as:

$$C_{\text{Water}} (\text{g m}^{-2}) = (\text{TOC} + \text{DIC}) \times Z - C_{\text{Alg}} (\text{g m}^{-2}), \quad (8)$$

and

$$N_{\text{Water}} (\text{or } P_{\text{Water}}) (\text{g m}^{-2}) = \text{TN} (\text{or } \text{TP}) \times Z - N_{\text{Alg}} (\text{or } P_{\text{Alg}}) (\text{g m}^{-2}). \quad (9)$$

C_{Alg} , N_{Alg} , and P_{Alg} are concentrations of elements stored in tissue of phytoplankton, calculated as:

$$C_{\text{Alg}} (\text{or } N_{\text{Alg}}, P_{\text{Alg}}) = B_{\text{Alg}} \text{DW} \times C\%_{\text{Alg}} (\text{or } N\%_{\text{Alg}}, P\%_{\text{Alg}}), \quad (10)$$

where $B_{\text{Alg}} \text{DW}$ is dry biomass of phytoplankton calculated as $\text{Chl-}a \times 70 \times Z/1000$ (Scheffer 1998) and Z is water depth. $C\%_{\text{Alg}}$, $N\%_{\text{Alg}}$, and $P\%_{\text{Alg}}$ are the elemental percentages of the phytoplankton biomass and averaged 34.0%, 5.50%, and 1.14%, respectively, based on the literature values (Appendix Table S1).

The decomposition rates of macrophytes and phytoplankton were collected from literature (Appendix Table S2). Decomposition rates (k , natural log units d^{-1}) were described from the changes in plant dry weight (W) with time (t , d) since the initiation of the experiments using the equation $W_t = W_0 e^{-kt}$, the model most often used in the literature (Olson 1963). The value of k is highly dependent on the incubation days; the longer plant tissues are incubated, the higher k is for specific species in specific

Table 2. Basic statistics of the related limnological parameters in the study lakes. B_{Mac} = wet biomass of submersed macrophytes; Chl-*a* = phytoplankton chlorophyll *a* concentration; TN and TP = total nitrogen and phosphorus concentration of lake water, respectively; TN_{Sed} , TP_{Sed} , and OM_{Sed} = concentrations of TN, TP, and organic matter in sediment, respectively. SE = standard error.

		B_{Mac} , g m ⁻²	Chl- <i>a</i> , μg L ⁻¹	TN, μg L ⁻¹	TP, μg L ⁻¹	TN_{Sed} , g kg ⁻¹	TP_{Sed} , g kg ⁻¹	OM_{Sed} , g kg ⁻¹
<i>P. crispus</i>								
present (<i>n</i> = 20)	Minimum	6	0.8	82	9	2.37	0.43	31.7
	Mean	427	11.3	1488	35	3.55	0.71	54.8
	Median	194	9.2	656	28	3.47	0.69	54.4
	Maximum	2798	46.2	4587	119	6.34	1.23	92.6
	SE	153	2.27	348	5.6	0.21	0.04	3.9
<i>P. crispus</i>								
absent (<i>n</i> = 40)	Minimum	—	3.2	215	16	1.48	0.36	25.1
	Mean	—	49.4	1400	65	3.41	0.68	67.0
	Median	—	22.3	918	68	3.45	0.65	63.6
	Maximum	—	306.6	4478	157	5.18	1.20	116.2
	SE	—	11.5	190	4.7	0.15	0.03	3.6
<i>P. maackianus</i>								
present (<i>n</i> = 26)	Minimum	3	0.4	25	5	2.67	0.20	43.7
	Mean	3336	15.7	829	47	5.75	0.56	113.6
	Median	2037	3.1	566	39	5.94	0.55	114.1
	Maximum	13 592	85.9	5365	165	8.13	0.71	176.5
	SE	749	4.7	224	7.7	0.29	0.02	7.0
<i>P. maackianus</i>								
absent (<i>n</i> = 54)	Minimum	—	1.5	104	19	1.78	0.51	35.0
	Mean	—	70.0	827	147	5.30	0.80	98.7
	Median	—	61.5	838	119	5.42	0.77	97.3
	Maximum	—	185.2	1722	385	8.18	1.48	147.8
	SE	—	6.1	59.7	15.6	0.18	0.02	3.7

experiment; therefore, only experiments with an incubation length of ~2 months (56–72 days) were included in our literature review. For experiments lasting longer than 2 months, we collected the original data whenever possible and calculated the decomposition rate in that timespan only.

The subsequent decomposition rates were based on weight loss of plant tissue placed in litter bags. Although insightful, these experiments failed to reproduce natural decomposition rates because of limited access of detritivores to the organic matter in the bags; therefore, we analysed plant residues (detritus) in the sediment at different intervals after the macrophyte die-off. During macrophyte presence, data of detritus were not included because distinguishing between fresh plant tissue and detritus was not possible. *P. crispus* dies off in summer (usually in early July) and recovers in winter (usually in December); the months since the *P. crispus* die-off were

calculated from 1 July for all cases. The months since the *P. maackianus* die-off were calculated according to the time when plants disappeared (Table 1).

Lakes where macrophytes were present at the sampling sites are further referred to as macrophyte-present; accordingly, a lake without macrophytes at the sampling sites is referred to as macrophyte-absent. As previously mentioned, 2 approaches were used to analyse the influences of alternative states on the functioning of lakes as C, N, and P stocks. To simplify, we henceforth refer to the approach based on long-term data of 9 years in the same lake (17–23 lake-months: Bao'ankou, Shuimiao, and Changlingtou; Table 1) as multi-year comparison and the approach based on data no longer than 4 years from 8 lakes as multi-lake comparison.

STATISTICA 8.5, SPSS 16.0, and Microsoft Excel 2010 were used for data processing and analyses, and an

unequal *n post hoc* ANOVA was used to test the differences between group means. Variance homogeneity was tested with the Levene's test before the ANOVA analysis. When the assumption of homogeneity was violated ($p < 0.05$), a nonparametric Welch test was performed to compare the means between groups.

Results

Basic limnological characteristics of the study lakes

Biomass of *P. crispus* was considerably lower (mean 427 g m⁻², median 194 g m⁻²) than that of *P. maackianus* (mean 3336 g m⁻², median 2037 g m⁻²; $p = 0.001$; Table 2). Chl-*a*, however, did not significantly differ between *P. crispus* and

P. maackianus lakes when macrophytes were present ($p = 0.41$) or absent ($p = 0.09$). The differences in TN and TP between *P. crispus* and *P. maackianus* lakes were not significant when macrophytes were present ($p = 0.13$ and 0.24, respectively) but were significant when macrophytes absent ($p = 0.006$ and <0.001). Sediment characteristics (TN_{Sed}, TP_{Sed}, and OM_{Sed}) differed significantly between *P. crispus* and *P. maackianus* lakes when macrophytes were present ($p < 0.001$) and absent ($p < 0.001$, $p = 0.003$, and $p < 0.001$, respectively), with higher concentrations of N, P, and OM in *P. maackianus* lakes. Two-way ANOVA showed that the interaction effects of species and presence/absence were statistically significant on TP ($F = 6.30$, $p = 0.01$), TP_{Sed} ($F = 18.76$, $p < 0.001$), and OM_{Sed} ($F = 7.93$, $p = 0.006$) but not on Chl-*a* ($F = 0.83$, $p = 0.36$), TN ($F = 0.05$, $p = 0.82$), and TN_{Sed} ($F = 0.50$, $p = 0.48$).

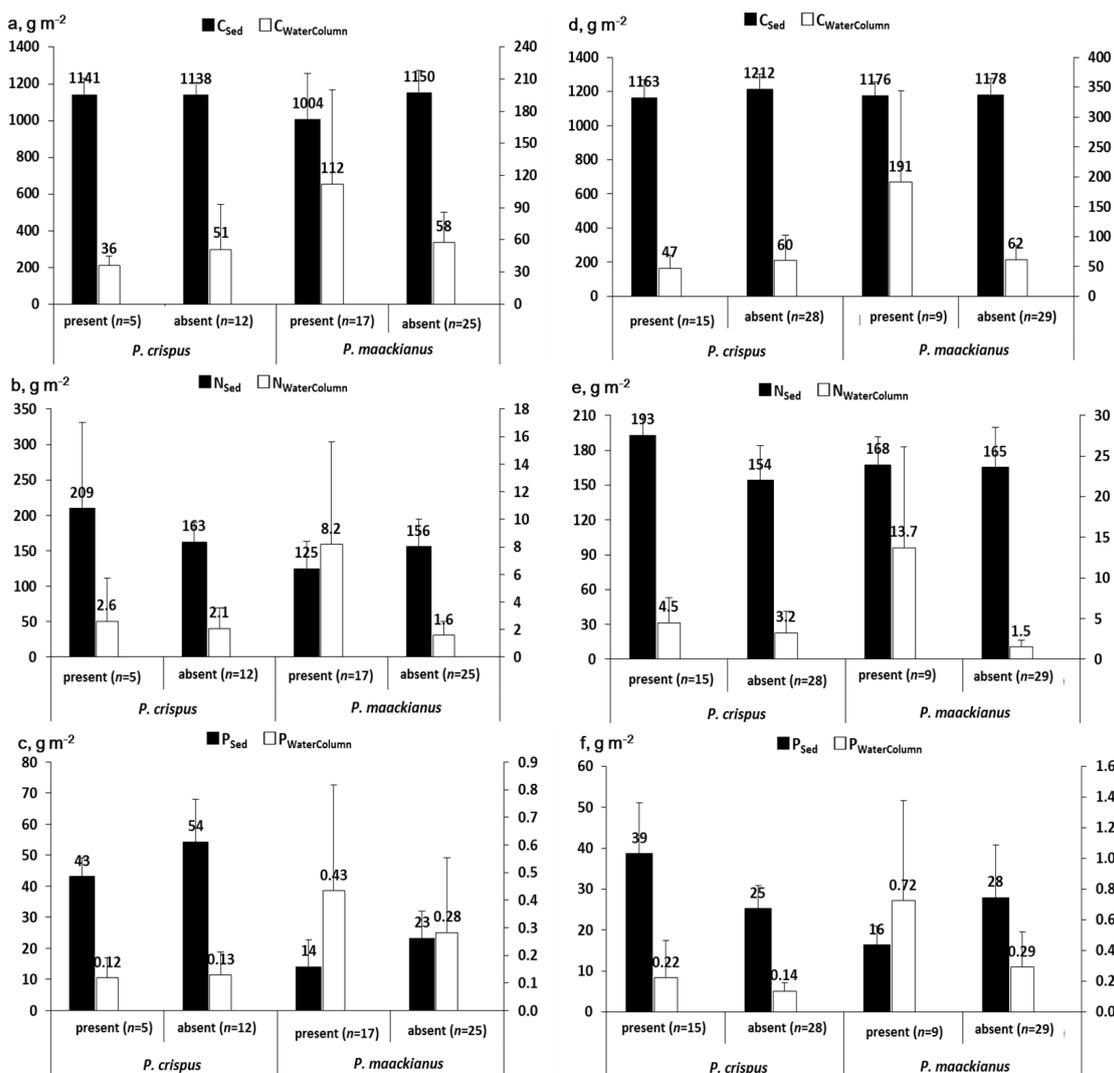


Fig. 3. Stocks (mean and standard deviation) of carbon, nitrogen, and phosphorus in the sediments (C_{Sed}, N_{Sed}, P_{Sed}) and the water column (C_{WaterColumn}, N_{WaterColumn}, P_{WaterColumn}) during macrophyte-present and macrophyte-absent in lakes with *Potamogeton crispus* or *P. maackianus* in (a–c) a multi-year comparison and (d–f) multi-lake comparison. The water column stocks include the elements dissolved and suspended in the water and those incorporated in macrophytes.

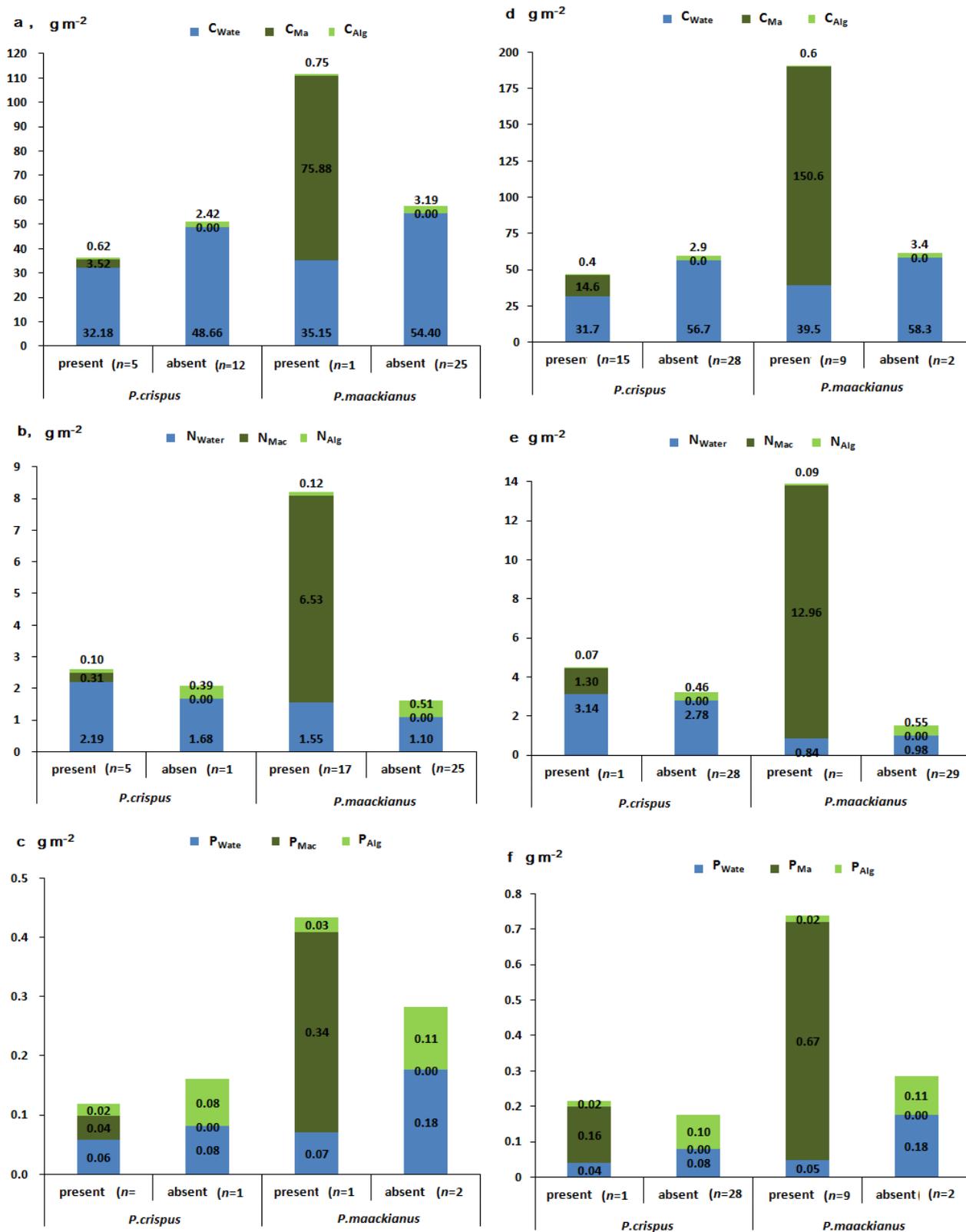


Fig. 4. Stocks (mean) of carbon, nitrogen, and phosphorus in water (C_{Water} , N_{Water} , P_{Water}), macrophytes (C_{Mac} , N_{Mac} , P_{Mac}), and phytoplankton (C_{Alg} , N_{Alg} , P_{Alg}) during macrophyte present and absent in lakes supporting *Potamogeton crispus* and *P. maackianus* in (a–c) a multi-year comparison and (d–f) multi-lake comparison.

Stocks of carbon, nitrogen, and phosphorus in sediments and water columns

In the multi-year comparison of *P. crispus* lakes, the elemental concentrations in sediment and the water column did not differ significantly (C_{Sed} $p = 0.94$; N_{Sed} $p = 0.28$; P_{Sed} $p = 0.11$; $C_{\text{WaterColumn}}$ $p = 0.46$; $N_{\text{WaterColumn}}$ $p = 0.63$; $P_{\text{WaterColumn}}$ $p = 0.78$) when macrophytes were present or absent (Fig. 3a–c). The multi-lake comparison showed similar results (Fig. 3d–f), except with significantly lower N_{Sed} ($p < 0.001$) and P_{Sed} ($p = 0.001$) when macrophytes were absent (C_{Sed} $p = 0.12$; $C_{\text{WaterColumn}}$ $p = 0.28$; $N_{\text{WaterColumn}}$ $p = 0.16$; $P_{\text{WaterColumn}}$ $p = 0.20$).

In *P. maackianus* lakes, significant differences between the contrasting states were found for almost all the variables in the multi-year comparison. Sediment C, N, and P concentrations were significantly higher after die-off of the macrophytes ($p = 0.04$, 0.02 , and 0.002 for C_{Sed} , N_{Sed} , and P_{Sed} , respectively) whereas the C, N, and P concentrations in the water column (including the elemental stock in the macrophytes) were generally higher when the macrophytes were still present ($p = 0.02$, 0.002 , and 0.14 for $C_{\text{WaterColumn}}$, $N_{\text{WaterColumn}}$, and $P_{\text{WaterColumn}}$, respectively). In the multi-lake comparison, all variables were also found to differ significantly, with the exception of C_{Sed} ($p = 0.94$) and N_{Sed} ($p = 0.86$). P_{Sed} was higher when the macrophytes had disappeared ($p = 0.04$), and elemental concentrations in the water column were higher when the macrophytes were present ($C_{\text{WaterColumn}}$ $p = 0.04$; $N_{\text{WaterColumn}}$ $p = 0.02$; $P_{\text{WaterColumn}}$ $p = 0.08$).

Two-way ANOVA showed that the interaction effects of species and presence/absence were statistically significant on TN_{Sed} ($F = 19.00$, $p < 0.001$), TP_{Sed} ($F = 14.23$, $p < 0.001$), $C_{\text{WaterColumn}}$ ($F = 19.07$, $p < 0.001$), and $N_{\text{WaterColumn}}$ ($F = 20.64$, $p < 0.001$) but not on C_{Sed} ($F = 2.05$, $p = 0.15$) and $P_{\text{WaterColumn}}$ ($F = 3.44$, $p = 0.07$).

When looking at the temporal dynamics of elements along with the months after the die-off of *P. crispus*, no significant trend was found for the concentrations in the sediment (Spearman rank correlation, $p = 0.13$ – 0.94); a highly significant decreasing trend was found for $C_{\text{WaterColumn}}$ ($p < 0.001$), a slightly significant decreasing trend was found for $P_{\text{WaterColumn}}$ ($p = 0.04$), and no significant trend was found for $N_{\text{WaterColumn}}$ ($p = 0.56$). A focus on the dynamics of $C_{\text{WaterColumn}}$ showed that the highly significant decreasing trend was due to the extremely high value immediately following (0.5 month) the die-off of macrophytes, averaging 125.5 g m^{-2} (50.7 – 185.2 g m^{-2}); the dynamic after 0.5 month was not obvious, varying between 22.5 and 66.1 g m^{-2} . For *P. maackianus* lakes, no significant trend was found for any variable, with the exception of a slightly increasing trend

of P_{Sed} ($p = 0.01$). In summary, the general patterns (Fig. 3) would not be fundamentally altered by the temporal dynamics of elements along with the time after the die-off of macrophytes.

Stocks of carbon, nitrogen, and phosphorus in the different water column components

The biomass of *P. maackianus* was much higher than that of *P. crispus*, leading to higher C (15.9 times), N (15.5 times), and P (6.3 times) for macrophyte stocks in *P. maackianus* lakes than in *P. crispus* lakes ($p < 0.001$ for both the multi-year and the multi-lake approaches; Fig. 4). Elemental stocks in phytoplankton (C_{Alg} , N_{Alg} , and P_{Alg}) and water (C_{Water} , N_{Water} , and P_{Water}) did not significantly differ between *P. crispus* and *P. maackianus* lakes ($p = 0.07$ – 0.34). When macrophytes were absent, no significant difference was found for elemental stocks in the water ($p = 0.36$ – 0.65) between *P. crispus* and *P. maackianus* lakes, with the exception of N_{Water} and P_{Water} , which were significantly lower/higher in the *P. crispus* lakes in the multi-lake comparison ($p = 0.001$ and $p < 0.001$, respectively).

When shifting from macrophyte-presence to phytoplankton-absence, both the multi-year and multi-lake comparison showed a significant increase in phytoplankton biomass and the elemental stocks inferred from it, with the exception of the multi-year comparison in *P. crispus* lakes ($p = 0.38$). For the dissolved elements in water, C_{Water} and P_{Water} increased both in *P. crispus* lakes (C_{Water} : $p = 0.35$ for multi-year and 0.002 for multi-lake; P_{Water} : $p = 0.58$ for multi-year and 0.04 for multi-lake) and *P. maackianus* lakes (C_{Water} : $p = 0.02$ for multi-year and 0.03 multi-lake; P_{Water} : $p = 0.02$ for multi-year and 0.007 for multi-lake), whereas N_{Water} decreased or slightly increased ($p = 0.33$ – 0.70 for all cases). When summarizing suspended and dissolved components (i.e., mobile pool), the amounts of C ($C_{\text{Water}} + C_{\text{Algae}}$) increased by an average of 1.71-fold after *P. crispus* die-off and by 1.57-fold after *P. maackianus* die-off; P ($P_{\text{Water}} + P_{\text{Algae}}$) increased by 2.52-fold and 3.61-fold, respectively.

Two-way ANOVA showed no statistically significant interaction effects of species and presence/absence on elemental concentrations of algae ($F = 0.12$ – 0.14 , $p = 0.71$ – 0.73) and water ($F = 0.04$ – 3.35 , $p = 0.07$ – 0.84).

Coarse detritus (>6.35 μm) in sediments

After the die-off of *P. crispus*, the coarse detritus in the top sediment (hereafter detritus; mean 324 g m^{-2} , median 294 g m^{-2} , $n = 46$) was significantly lower ($p < 0.001$) than in *P. maackianus* lakes (mean 560 g m^{-2} , median 565 g m^{-2} , $n = 80$). Notwithstanding the high variation,

detritus content of *P. crispus* lakes and *P. maackianus* lakes showed significantly different dynamics over time (ANCOVA analysis, $F = 68.27$, $p < 0.001$; Fig. 5a). Detritus decreased rapidly with time in *P. crispus* lakes but remained high in *P. maackianus* lakes, and began to decline around 70–80 months after die-off. Focusing on the dynamics in individual lakes (Fig. 5b), the initial detritus content in *P. crispus* lakes varied strongly among lakes soon after the die-off (average 506 g m^{-2} , range

$180\text{--}796 \text{ g m}^{-2}$) and less so after 8.5 months (average 161 g m^{-2} , range $55\text{--}396 \text{ g m}^{-2}$). Most important, the sediment detritus content showed a decreasing trend in all lakes. The pattern in *P. maackianus* lakes is harder to interpret because a continuous data series is lacking within individual lakes. In lakes monitored up to 70 months after the die-off, no decrease in detritus was found, whereas in lakes where monitoring started 70 months after die-off, a considerable decrease was found.

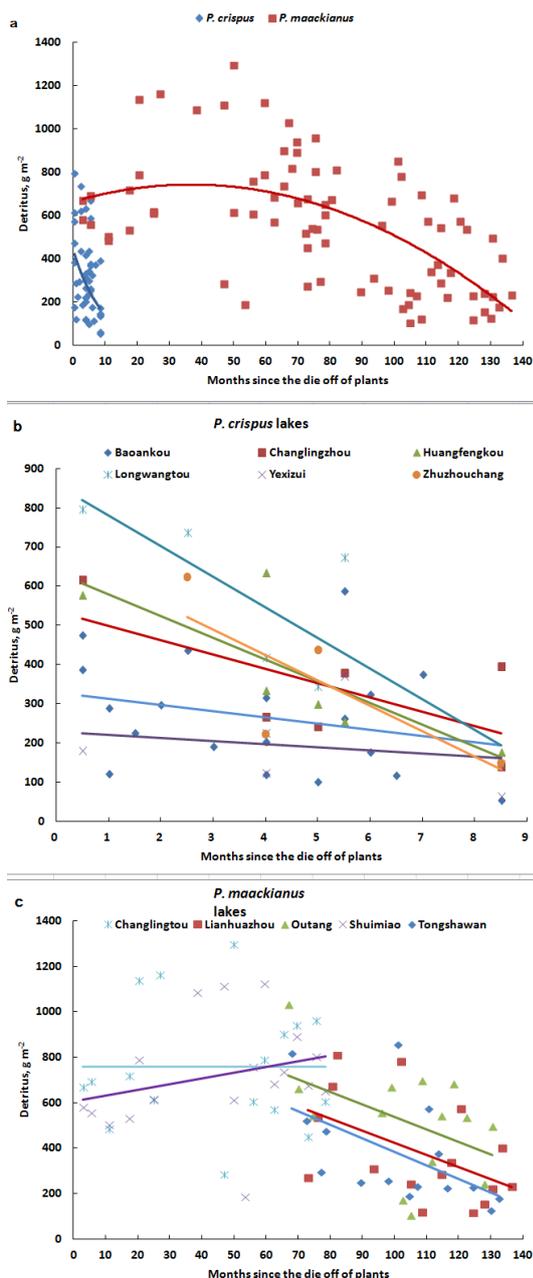


Fig. 5. Regressions of coarse detritus ($>6.4 \mu\text{m}$) in the sediments against months since the plant die-off in lake groups supporting (a) *P. crispus* lakes and *P. maackianus* and specific lakes supporting (b) *P. crispus* and (c) *P. maackianus*.

Discussion

Reallocation of elemental stocks in water column and sediment after shifts in alternative states

Elemental concentrations in the water column and in the sediment differed between *P. maackianus* present and absent states (Fig. 3). This outcome supports our hypothesis (hypothesis 1) that shifts between dominant primary producers not only change the functioning of lake P and N stocks, but of C stock as well by reallocating elements in water the column and sediment. All elemental stocks in the sediment increased significantly, with the exception of nonsignificant changes in C and N concentrations in the multi-lake comparison, whereas elemental stocks in the water column decreased significantly, with the exception nonsignificant changes in P in the multi-year comparison.

Although our approach does not identify underlying causes, the significantly lower ($p < 0.001$) decomposition rate of *P. maackianus* (0.01 d^{-1}) compared to phytoplankton (averaged 0.05 d^{-1} ; Appendix Table S1; Fig. 1) provides a likely explanation. After die-off, the macrophyte biomass accumulates in the sediments, thereby increasing sediment elemental concentrations. Elemental concentrations in the top sediment may have further increased by the sedimentation of phytoplankton. Although phytoplankton has a higher decomposition rate, lower oxygen conditions at the sediment–water interface associated with primary producer regime shifts (Scheffer 1998) may have prevented fast decomposition. In a temperate shallow eutrophic lake, lower mineralization rates were also thought to be related to a decrease in benthic oxygen coinciding with a loss of submersed macrophytes (Brothers et al. 2013).

Different patterns of elemental reallocation between lake types

No marked elemental reallocation in water column and sediment occurred in *P. crispus* lakes when switching to plant absence (Fig. 3 and 4), supporting our hypothesis (hypothesis 2) that lakes losing rapidly decomposing

macrophytes increase their sediment stocks to a lesser extent than lakes losing slowly decomposing macrophytes. The faster decrease in coarse detritus in *P. crispus* lakes than in *P. maackianus* lakes after macrophytes die-off further confirmed the notion that loss of rapidly decomposing macrophytes has a smaller effect on elemental stocks than the loss of more recalcitrant species (Fig. 5).

Additionally, differences in biomass and growing structure may play a role. *P. maackianus* is a perennial species able to overwinter, and its biomass builds up over years. Comparatively, *P. crispus* is an annual species characterized by total die-off after early summer. Therefore, *P. maackianus* inherently tends to have a higher biomass than *P. crispus* and reallocates more elements from the water column to the sediment after die-off. This reallocation takes place up to months after die-off because *P. maackianus* plants stay largely upright after death, unlike *P. crispus* plants that collapse more quickly. To test whether loss of *P. crispus* can cause marked elemental reallocation in water column and sediment when the biomass is high, 6 lakes with *P. crispus* biomass of higher than the median (194 g m⁻²) were further selected to compare the situation before and after the plant die-off (see comparison with test shown in Appendix Fig. S1). The results were similar to those found in the full dataset (Fig. 3), characterized by minor effects on elemental reallocation. We therefore argue that the contrasting influences on elemental reallocation between species originate from a combination of differences in their biomass and decomposition rates.

Implications of changed functioning of lakes as stocks of carbon, nitrogen, and phosphorus

Because the proportion of external loading retained in lakes tends to remain relatively constant, the outflow of nutrients, specifically that of P, tends to increase with eutrophication (Koiv et al. 2011). Our data show that macrophyte loss will further enhance this C and P outflow because of a decrease in C and P retention. Macrophyte loss tended to change the functioning of lakes as a place for elemental retention by increasing the mobile pool of C 1.5–1.9 times and the mobile pool of P 2.0–4.3 times. The mobile pool of N, however, tended to stay unchanged or decreased, with the decrease likely due to enhanced denitrification. Taken together, this finding implies a disproportional increase in C and P loading to downstream sites after macrophyte loss. Assuming that originally 40% of the small- to medium-sized (<500 km²) mid-lower Yangtze shallow lakes (total area 8740 km²) were occupied by *P. crispus* and 60% by *P. maackianus*, a complete macrophyte loss would mobilize high quantities

of C and P (roughly 1.9×10^5 and 1.4×10^3 tons, respectively). This mobilization could have cascading effects when causing eutrophication effects downstream, triggering further macrophyte loss that in turn may mobilize more nutrients. The problem may be exacerbated in a monsoon area where the rainfall is concentrated in later spring and summer but rare in late autumn and winter. The nutrients accumulated and concentrated in dry season may easily flush downstream during the wet season.

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Supplementary material i

Tables S1, S2; Figure S1 and references are available to download via the Inland Waters website, <https://www.fba.org.uk/journals/index.php/IW/issue/view/128>