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A regime shift from macrophyte to phytoplankton dominance enhances carbon burial in a shallow, eutrophic lake

Soren M. Brothers,[1,2,†] Sabine Hilt,[1] Katrin Attermeyer,[3] Hans Peter Grossart,[2,3] Sarian Kosten,[1,4] Betty Lischke,[2] Thomas Mehner,[1] Nils Meyer,[5] Kristin Scharnweber,[1] and Jan Köhler[1]

[1] *Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Müggelseedamm 301, Berlin 12587 Germany*
[2] *Institute for Biochemistry and Biology, Potsdam University, Potsdam 14476 Germany*
[3] *Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Alte Fischerhütte 2, Stechlin 16775 Germany*
[4] *Department of Aquatic Ecology and Environmental Biology, Radboud University Nijmegen,*
Heyendaalseweg 135, 6525AJ Nijmegen, The Netherlands
[5] *Department of Ecology, Berlin University of Technology, Berlin 10587 Germany*

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Abstract. Ecological regime shifts and carbon cycling in aquatic systems have both been subject to increasing attention in recent years, yet the direct connection between these topics has remained poorly understood. A four-fold increase in sedimentation rates was observed within the past 50 years in a shallow eutrophic lake with no surface in- or outflows. This change coincided with an ecological regime shift involving the complete loss of submerged macrophytes, leading to a more turbid, phytoplankton-dominated state. To determine whether the increase in carbon (C) burial resulted from a comprehensive transformation of C cycling pathways in parallel to this regime shift, we compared the annual C balances (mass balance and ecosystem budget) of this turbid lake to a similar nearby lake with submerged macrophytes, a higher transparency, and similar nutrient concentrations. C balances indicated that roughly 80% of the C input was permanently buried in the turbid lake sediments, compared to 40% in the clearer macrophyte-dominated lake. This was due to a higher measured C burial efficiency in the turbid lake, which could be explained by lower benthic C mineralization rates. These lower mineralization rates were associated with a decrease in benthic oxygen availability coinciding with the loss of submerged macrophytes. In contrast to previous assumptions that a regime shift to phytoplankton dominance decreases lake heterotrophy by boosting whole-lake primary production, our results suggest that an equivalent net metabolic shift may also result from lower C mineralization rates in a shallow, turbid lake. The widespread occurrence of such shifts may thus fundamentally alter the role of shallow lakes in the global C cycle, away from channeling terrestrial C to the atmosphere and towards burying an increasing amount of C.

Key words: calcite precipitation; CO_2 emissions; global carbon cycle; metabolism; regime shift; sedimentation; submerged macrophytes; temperate zone; trophic status.

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† **E-mail:** soren.brothers@igb-berlin.de

INTRODUCTION

Knowledge of the transport pathways of carbon (C) through the biosphere is central to understanding and predicting contemporary global changes in atmospheric carbon dioxide (CO_2) concentrations. In recent decades, our understanding of the significance of lakes and reservoirs for the global C cycle has dramatically improved, and it is currently believed that over a timespan of centuries to millennia, such systems globally bury two times more organic C than oceans (Dean and Gorham 1998). At the same time, CO_2 emissions from lakes to the atmosphere are estimated to be typically four or more times greater than lake C burial rates, with potential implications for global atmospheric CO_2 dynamics (Duarte and Prairie 2005, Cole et al. 2007). Researchers are therefore attempting to better understand and quantify the fundamental processes that influence C burial and emissions in lakes (e.g., Tranvik et al. 2009).

Ecological regime shifts are a widespread phenomenon across a variety of ecosystem types (e.g., Barnosky et al. 2012), yet their effects on the global C cycle remain poorly understood. In shallow lakes, a shift from a clear-water regime dominated by submerged macrophytes to a turbid one dominated by phytoplankton represents a fundamental transformation of a lake's ecological structure (Scheffer et al. 1993, Tranvik et al. 2009). The loss of a submerged macrophyte community in a shallow lake often increases benthic resuspension (Vermaat et al. 2000), and lowers water clarity (influencing benthic light availability) due to a higher availability of nutrients for phytoplankton production (e.g., Kufel and Ozimek 1994). By changing both abiotic and biotic characteristics of a lake, it is likely that a regime shift alters C cycling, and that C burial and emission rates of lakes may reflect these changes (e.g., Hobbs et al. 2012). Regime shifts in shallow lakes may thus be responsible for previously unconsidered processes which could potentially influence long-term changes in global atmospheric CO_2 concentrations as well as local organic C availability in aquatic ecosystems.

One complication which arises when identifying the effects of regime shifts comes from their frequently overlapping relationship to eutrophication. Regime shifts from macrophyte dominance to phytoplankton dominance in shallow lakes are often induced by increasing nutrient concentrations (e.g., Carpenter and Lathrop 2008), though at intermediate nutrient concentrations can also be triggered by disturbances (Jeppesen et al. 1990, Scheffer et al. 2001). Nevertheless, studies of regime shifts tend to focus on ecosystems across broad nutrient gradients, potentially obscuring the effect of changes in plant community structure alone. Nutrient enrichment has been widely correlated to decreases in lake heterotrophy (thus indicating a decline in ecosystem respiration relative to gross primary production, GPP) as evidenced by declining $p\mathrm{CO}_2$ and increasing surface oxygen (O_2) concentrations (del Giorgio et al. 1999, Kosten et al. 2010, Balmer and Downing 2011). Heathcote and Downing (2012) and Heathcote et al. (2013) both identify a strong link between watershed erosion and C burial rates in lakes, though Heathcote and Downing (2012) further observe that watershed fertilization (and thus nutrient enrichment) appears to propel a major fraction of this increased C burial. Elevated phytoplankton production is thus a common factor contributing to high C burial rates in such systems (Heathcote and Downing 2012). However, the degree to which these broad differences can be attributed to changes in corresponding regime shifts as opposed to changes in nutrient availability is difficult to say. This is especially the case with shallow lakes, as studies by Vadeboncoeur et al. (2008) and Blindow et al. (2006) have shown that a loss of benthic primary production with eutrophication may be anticipated with a shift from a clear-water to a turbid regime, potentially outweighing the positive effects of eutrophication on pelagic primary production. In such instances, a decline in heterotrophy following a shift to phytoplankton dominance would not, theoretically, result from an increase in whole-lake primary production, but rather from a decrease in respiration (i.e., C mineralization) rates. This presents an alternative mechanism for elevated C burial rates in shallow eutrophic lakes, mediated primarily by changes in plant community structure, rather than ambient nutrient concentrations.

In order to better understand the relationship between regime shifts and carbon cycling, we compared two shallow, eutrophic lakes featuring

Table 1. General characteristics of the two study lakes in northeast Germany (mean ± SE): phytoplankton-dominated Gollinsee and macrophyte-dominated Schulzensee.

	Gollinsee		Schulzensee		
Factor	Measurement	*n*	Measurement	*n*	*p*
Surface area (m^2)	33,000		39,000		...
Z_{mean} (m)	1.7		2.2		...
Z_{max} (m)	2.9		4.2		...
$Z_{secchi\ mean}$ (m)	1.4 ± 0.1	17	1.9 ± 0.1	16	<0.001
pH	7.9 ± 0.1	20	7.6 ± 0.1	20	0.003
Chlorophyll *a* (µg/L)	23 ± 3	21	13 ± 3	19	0.02
Summer benthic O_2 (%)†	9 ± 8	7	37 ± 10	5	0.049
Total phosphorus (µg/L)‡	42 ± 3	20	34 ± 3	20	0.13
Soluble reactive phosphorus (µg/L)‡,§	4.7 ± 0.6	13	4.4 ± 0.6	13	0.70
Total nitrogen (mg/L)‡	1.2 ± 0.14	3	0.9 ± 0.06	17	0.07
Dissolved organic carbon (mg/L)‡	12.3 ± 0.3	16	11.3 ± 0.3	18	0.02
Dissolved inorganic carbon (mg/L)‡	32.2 ± 0.4	20	33.6 ± 0.4	20	0.01

† Calculated from June, July, and August vertical profiles.
‡ Epilimnetic, pelagic means.
§ One high outlier excluded in Gollinsee.

alternative plant community structures at similar ambient nutrient concentrations. We here considered two prime hypotheses. First, regarding the net outcome of regime shifts on the C cycling characteristics of these lakes, we predicted that our phytoplankton-dominated study lake would feature higher rates of C burial than the macrophyte-dominated study lake, despite similar nutrient concentrations. To test this, we calculated a C mass balance (adapted from Andersson and Sobek 2006) which examined the annual C loading and losses (via groundwater export, burial, or surface emissions) of each lake. As our phytoplankton-dominated study lake had undergone a regime shift involving a loss of submerged macrophytes within the past five decades (identified from dated macrofossil remains), we expected changes in C burial rates to be linked to this ecological regime shift. Our second hypothesis was that the process behind an increase in C burial would be the result of a relative decline in ecosystem respiration (ER) compared to whole-lake GPP in the phytoplankton-dominated lake. To identify the mechanisms behind differences in C burial rates between lakes, we calculated the C burial efficiency (defined as C burial divided by C deposition; Sobek et al. 2009) as well as ecosystem C budgets (adapted from Andersson and Sobek 2006) for each lake. C burial efficiency calculations identify the fraction of C which remains in the sediments once being deposited there, while the ecosystem C budgets identify the metabolic differences between the study lakes by comparing organic carbon gains (as external loading or internal primary production) and losses (via groundwater export, burial, or mineralization). Based on a previous study (Brothers et al. 2013) that identified a lower annual whole-lake primary production in this phytoplankton-dominated lake compared to the macrophyte-dominated system during the same study period, we hypothesized that the relative decline in ER compared to GPP (and thus lower heterotrophy) in the phytoplankton-dominated lake would be due to a decline in C mineralization rates rather than an increase in GPP.

MATERIALS AND METHODS

Study sites and sampling

Kleiner Gollinsee (53°01′ N, 13°35′ E, hereafter referred to as Gollinsee) is a eutrophic, turbid lake without submerged macrophytes (Table 1). Schulzensee (53°14′ N, 13°16′ E) is a similarly sized eutrophic lake which exhibits greater water clarity than Gollinsee (Table 1), along with a substantial submerged macrophyte community (predominantly the non-rooted *Ceratophyllum submersum* L.). Both lakes have distinct open-water (pelagic) and littoral zones. The littoral zones are dominated by floating-leaved water lilies (primarily *Nymphaea alba* L.) and shoreline reed belts (*Phragmites australis* Trin. Ex Steud.). Both are hard-water, calcium-rich lakes located in the low-lying rural region of northeastern Germany, and have no sizeable surface in- or outflows. Furthermore, both lakes are located in forested watersheds dominated by pine trees (*Pinus sylvestris*), and are completely encircled by alder trees (*Alnus glutinosa* L.).

A comparison of Secchi disk readings, dissolved organic carbon (DOC) concentrations, and chlorophyll *a* (chl *a*) concentrations (by *t*-test) indicated that Secchi depths in our study lakes were much better predicted by phytoplankton chl *a* concentrations ($r^2 = 0.37$, $p < 0.001$) than DOC ($r^2 = 0.005$, $p = 0.79$). As chl *a* concentrations were significantly higher in Gollinsee (mean = 23 μg/L) than in Schulzensee (mean = 13 μg/L; *t*-test, $p = 0.02$, Table 1), and phytoplankton was the only biotic factor controlling the light available to benthic primary production, we here refer to Gollinsee as phytoplankton-dominated. We here refer to Schulzensee as a macrophyte-dominated lake, following literature which has suggested that its areal coverage of submerged macrophytes (20–25%) is sufficient to significantly suppress phytoplankton (Hilt and Gross 2008) and boost zooplankton (Thoms et al. 1999), thus influencing water clarity and benthic productivity.

Littoral and pelagic water samples were taken every four weeks throughout the sampling period (early April 2010 to early April 2011). Pelagic samples generally included equal portions of water from 0.5 m, 1 m, and 2 m, while littoral samples were a mixture of subsurface ($Z = 0.5$ m) water from three random locations within the reed belt. Samples were transported to the laboratory in a dark cooler, and were analyzed within 12 to 24 hours of sampling. Secchi depths were recorded during each sampling visit, along with vertical profiles of O_2 concentrations, pH, and temperature using a Yellow Springs Instruments (YSI) monitoring probe (Xylem Inc., Yellow Springs, OH, USA). Water samples were analyzed for concentrations of total phosphorus (TP), soluble reactive phosphorus (SRP), and total nitrogen (TN), DOC, and dissolved inorganic carbon (DIC) following standard procedures.

Sedimentation

Sediment cores (65 and 95 cm in length in Gollinsee and Schulzensee, respectively) were retrieved with Uwitec corers (9 cm diameter, Mondsee, Austria) from the open-water zone of each lake, at a location roughly halfway between the lake's center and shoreline. As sedimentation rates are often greatest at the deepest point of a lake (e.g., Petterson et al. 1993), our choice of coring location should reduce any systematic spatial bias in sedimentation rates. However, due to the similarity between maximum and mean depths (Table 1), the lack of surface in- or outflows, and the small size of both lakes, significant or systematic variations in sediment burial rates between lake sites are unlikely.

Sediment cores were sliced at each 1 cm depth, and sediment materials were stored in plastic cups sealed with Parafilm (M) to avoid moisture loss. Samples remained in a cool (~10°C), dark location until processing. Sediments were analyzed by Flett Research laboratories (Winnipeg, Canada) for Pb-210, Cs-137, and Ra-226 isotope signals to determine sedimentation rates for the past approximate 150 years. Separate cores were taken from proximate locations within each lake for determining loss-on-ignition (LOI) at 450°C for two hours (for organic C) and 900°C (for calcium carbonate), as well as direct organic and total C measurements by a vario EL CHNOS Element Analyzer (Elementar Analysensysteme, Hanau, Germany). Organic C (OC) calculated as 50% LOI (following Håkanson and Jansson 1983:316) was only applied to depths for which direct OC measurements were unavailable. The burial rates of OC, total C, and calcite were calculated as the product of the total sedimentation rate at a given depth (from dating) and the fraction which each element or compound constituted at the equivalent depth.

Dated sediment cores were used to quantify current and historic C burial rates in both lakes (for C balances), but to better understand the underlying process behind these data, C burial efficiency was also calculated (as C burial divided by C deposition, following Sobek et al. 2009). Sediment deposition rates were measured using two sediment traps installed at the center of each lake. Traps were stationed at the deepest point of each lake to minimize errors from resuspension (Bloesch and Uehlinger 1986). The trap was carefully installed at a depth at which the bottom of the trap was within approximately 30 cm of Z_{max} in order to reduce any direct disturbance of the sediment surface during

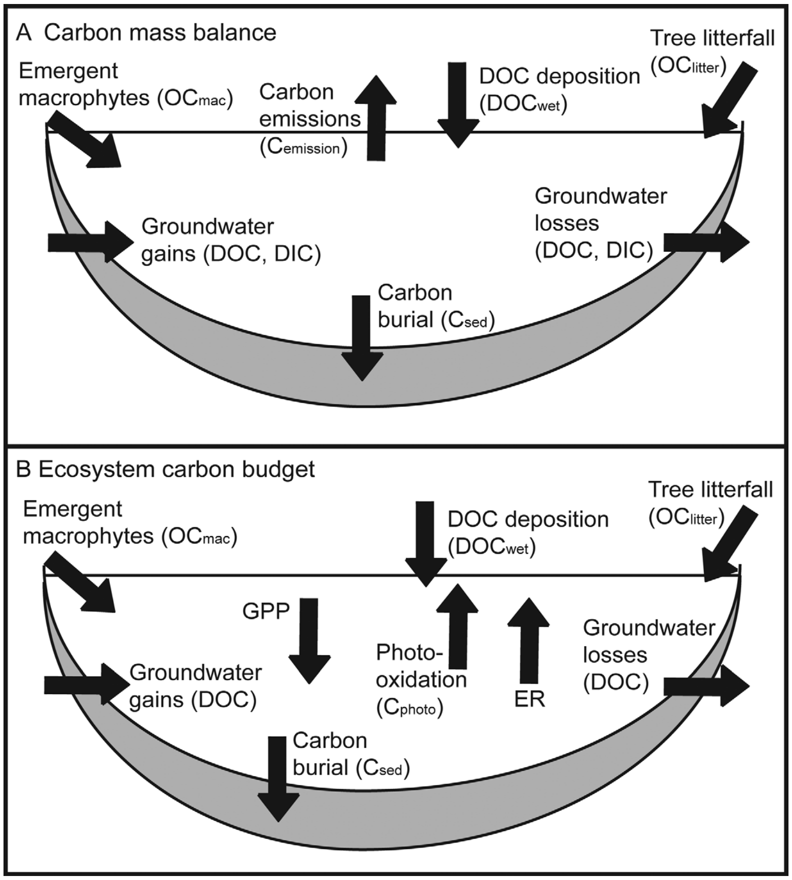

Fig. 1. Input and output variables for the (A) carbon mass balance and (B) ecosystem carbon budget approaches, adapted from Andersson and Sobek (2006). "Emergent macrophytes" here includes emergent and floating-leaved macrophytes.

installation. Resuspension was expected to be low, as both lakes were located in landscape depressions and surrounded by trees. Deposited material was collected biweekly throughout the ice-free period, and was immediately transported to the laboratory for filtration. The total C content of filters was measured by a CHNOS Element Analyzer.

Carbon balances

Our C mass balance assumes that the quantity of C entering each lake in one year (C_{in_M}) equals the quantity of C loss in the same year (C_{out_M}). This approach thus considers the lake as a black box where only the inputs (primarily from groundwater and surrounding vegetation) and outputs (via groundwater, surface emissions, or burial) are considered (Fig. 1A). As this approach considers only carbon entering and exiting the aquatic lake environment, C burial in the sediments (measured by dated sediment cores) is treated as a C loss. We adapted the methods of Andersson and Sobek (2006) for C mass balances and ecosystem budgets to our smaller systems. Our C mass balance is thus defined as:

$$DOC_{in} + DIC_{in} + OC_{litter} + DOC_{wet} + OC_{mac} = DOC_{out} + DIC_{out} + C_{emission} + C_{sed} \quad (1)$$

where DOC_{in} and DIC_{in} are the groundwater input of DOC and DIC, respectively, OC_{litter} is the C input from the litterfall of surrounding trees, DOC_{wet} (estimated as 1 g $C \cdot m^{-2} \cdot yr^{-1}$) is the DOC input from precipitation, and OC_{mac} is the C input by floating-leaved and emergent macrophytes, here considered allochthonous (following Andersson and Sobek 2006) as the C in these plants is primarily derived from the atmosphere. DOC_{out} and DIC_{out} represent the losses of DOC and DIC by groundwater, $C_{emission}$ represents the net C losses to the atmosphere (as CO_2), and C_{sed} represents C burial. Values are presented in $g\ C \cdot m^{-2} \cdot yr^{-1}$.

Our ecosystem C budget (also adapted from Andersson and Sobek 2006) assumes that the total quantity of organic C gained within a lake over the course of a year (OC_{in_E}) is equivalent to the total quantity of organic C processed or lost over the same time period (OC_{out_E}). While the C mass balance considers only the total inputs and outputs for each lake, the ecosystem C budget focuses on organic carbon gains and losses, and thus provides a higher internal resolution to the metabolic processes occurring within each lake, including carbon fixation and mineralization (Fig. 1B). We thus define our ecosystem C budget as:

$$DOC_{in} + OC_{litter} + DOC_{wet} + GPP = DOC_{out} + C_{photo} + C_{sed} + ER \qquad (2)$$

where GPP is annual gross primary production, C_{photo} is organic C loss by photo-oxidation, and ER is ecosystem respiration. Values are presented in $g\ C \cdot m^{-2} \cdot yr^{-1}$. Photo-oxidation was estimated to be 13.1 $g\ C \cdot m^{-2} \cdot yr^{-1}$, from a lake with a comparable productivity and Secchi depth to our study lakes (Granéli et al. 1996).

To quantify the net annual allochthonous C load for each lake, groundwater DOC and DIC concentrations were measured every two to four weeks from two wells constructed in the immediate vicinity of the lakes (four to six meters from the shore). Wells were three to four meters deep, and groundwater samples were extracted from two to three meters below the soil surface. Data from sixteen other piezometer wells were used to determine the groundwater flow direction (S. Rudnick, *unpublished data*). Shallow groundwater tables were compared to changes in lake water levels, precipitation (recorded continuously at each lake), and estimates of evapotranspiration, providing monthly estimates of the gain and loss of groundwater at each lake. Any loaded organic C produced using CO_2 from outside the aquatic environment was considered allochthonous. This includes leaves from trees (OC_{litter}) as well as floating-leaved (*N. lutea* and *N. alba*) and emergent (*P. australis*) macrophytes. OC_{litter} was estimated from floating leaf traps installed at multiple locations along the shore of each lake. For floating-leaved macrophytes, plant density was estimated per square meter, and the total surface area occupied was estimated by GIS mapping, using GPS data by mapping the habitat boundary of each macrophyte group. Lake coverage estimates were also available from direct measurements taken in 2007, and the mean value of both estimates was applied. To calculate the C contribution of *P. australis*, reeds growing within and directly beyond the lake shore were included to account for loading during periods of high water levels or by leaching into the shoreline sediments and groundwater. Detailed measurements of reed area and density per square meter were made along the periphery of each lake. Maximum (mid-July) biomass estimates involved 20 random samples of floating-leaved and emergent macrophytes. Macrophytes were cut at the sediment surface, dried at 60°C for two days, and weighed, following Andersson and Sobek (2006). The mean C content of water lilies (38.3 ± 0.6%, both lakes combined) was measured by a vario EL CHNOS Element Analyzer, and mean values for reeds (45.6 ± 1%) are applied from Mille-Lindblom et al. (2006). It was assumed that the maximum summer living organic C content of emergent and floating-leaved macrophytes was equivalent to the annual quantity of C loaded into the aquatic environment by these groups, following Andersson and Sobek (2006) and references therein.

Surface-to-air CO_2 fluxes are calculated throughout the study year by coupling estimated surface pCO_2 concentrations to pH and temperature profiles, using lake-center wind speed data recorded by ultrasound every 10 minutes by a meteo multiprobe (ecoTech, Bonn, Germany). Emission rates were calculated following methods outlined by Cole and Caraco (1998), and adjusted for chemical enhancement (the enhancement of CO_2 exchange with the atmosphere resulting from high pH levels) following methods outlined by Bade and Cole (2006), and references therein. The concentration of pCO_2 in surface waters was calculated from DIC concentrations, pH, and temperature, adjusting for the concentration of calcium ions ($CaCO_3^0$,

$CaHCO_3^+$, and $CaOH^+$) following Gelbrecht et al. (1998) and references therein. Conservative pCO_2 concentrations are calculated for each lake by accounting for a possible measured pH bias of 0.2 from DOC effects (Herczeg et al. 1985, Cole et al. 1994). Although methane (CH_4) emissions can be important to consider as a greenhouse gas released by lakes to the atmosphere, their contribution to the mass transfer of C is generally considered to be minor (e.g., Tranvik et al. 2009), and they are thus not included in this analysis. Reeds may channel CO_2 directly between the sediments and the atmosphere (Brix et al. 1996), but we here consider this process as external to the lake aquatic environment, and exclude it from our C emission estimates.

The whole-lake gross primary production (GPP) of these study lakes during this period was available from Brothers et al. (2013), who calculated annual GPP as the sum of rates for separate producer communities. Specifically, whole-lake GPP was considered to be the sum of GPP rates calculated separately for phytoplankton, periphyton (attached algae, including epiphyton growing on submerged plant surfaces and epipelon growing directly on the muddy sediments), submerged macrophytes (*C. submersum*), and cyanobacteria (*Aphanothece stagnina* (Sprengel) A. Braun, only in Schulzensee).

Ecosystem respiration

Ecosystem respiration (ER) was defined as the sum of the respiration rates of aquatic plants, bacteria (pelagic, biofilm, and sediment), zooplankton, macrozoobenthos, and fish. Although attempts were made to provide as accurate estimates as possible for ER, many values relied heavily on literature estimates of biomass-to-respiration conversion factors or growth efficiencies, and were furthermore summed together to provide a single value of ecosystem respiration. Therefore, no meaningful range of error could be presented for ER rates. Instead, we considered these to be first order estimates, whose ultimate utility would be to define the relative importance of different respiration groups in each lake, and to ascertain whether the general range in which ER calculations fell would fit within the ecosystem C budget.

Aquatic plant respiration rates (R) were calculated using literature values for separate producer groups (except for *A. stagnina*, for which R measurements were available), with further details provided in Brothers et al. (2013). Bacterial production was measured monthly in water samples, periphyton strips, and sediment samples (top 1 cm) after Simon and Azam (1989; water) and Buesing and Gessner (2003; periphyton and sediment). The full procedure is described in Attermeyer et al. (2013). Bacterial R was estimated from measured bacterial production values, applying a common bacterial growth efficiency of 30% to both lakes, which is typical for eutrophic lakes (e.g., Biddanda et al. 2001).

Zooplankton R was estimated from zooplankton biomass, using a biomass-to-respiration conversion factor of $0.115\ g\ C \cdot g\ C^{-1} \cdot d^{-1}$ (Andersson and Kumblad 2006). Zooplankton samples were taken monthly during ice-free periods from April 2010 to April 2011, from the pelagic (and on two occasions littoral) zones of each lake. A 40-L mixed epilimnetic water sample was used to provide a 50-mL sub-sample which was immediately fixed with acidified Lugol's solution (Hoehn et al. 1998) to stain the ciliates. The remaining water was filtered through a 55-μm mesh, and these crustacean samples were fixed with 4% sugar formalin (Haney and Hall 1973). Samples were counted at the genus or species level, and volume (ciliates and rotifers) or size (crustaceans) was measured at the LimSa Gewässerbüro (Konstanz, Germany). Regressions were used to calculate the individual C content based on volume or size. Specifically, Telesh et al. (1998) was applied for rotifers, Müller and Geller (1993) for ciliates, and Dumont et al. (1975) for crustaceans. A C content of 50% dry weight (dw) was assumed (Gaedke 1992 and references therein).

Macroinvertebrate R was estimated from biomass, using biomass-to-respiration conversion factors for separate macroinvertebrate groups (classified by feeding type) from Andersson and Kumblad (2006). As detailed estimates were unavailable for 2010, 2011 biomass measurements from eight samplings (mid-April to early November) were adopted. Samples were collected along a transect from the lakeshore to the center of the lake which included multiple habitat zones (eulittoral zone: 0–1 m; sublittoral zone: 1–2 m, and profundal: >2 m). As no macroinvertebrates were present in the profundal zones, we restricted further analyses to the littoral zones. We sampled a 0.6-m^2 area using a kick net of 250-µm mesh size and the substrate was fixed in ethanol. Species were determined to the lowest possible taxonomic division, and wet weight (ww) was determined on each sampling occasion. Analyses were focused upon the most abundant taxonomic groups. Literature values were used to correct for the effects of weight loss due to preservation in ethanol (Leuven et al. 1985, González et al. 2002, von Schiller and Solimini 2005, Wetzel et al. 2005). To convert to dw, we used measured ww/dw ratios, and C content was assumed to be 45% dw (Peters 1983, Wetzel 2001). To calculate the ash-free dw of gastropods, we measured species-specific traits (body length, shell width or shell height) of individuals from three samplings (April, June, and November 2011) and applied our own regressions (M. Mährlein, *unpublished data*).

Fish R was calculated from biomass estimates using a biomass-to-respiration conversion factor of 0.033 g C·[g C^{-1}]·d^{-1} (Andersson and Kumblad 2006). In October 2010 and 2011 standardized fishing campaigns were carried out using Nordic multi-mesh gillnets and electrofishing. Eight gillnets were set perpendicular to the shore line from dusk until dawn. Sampling by electrofishing was conducted by applying 15 dips for 15 seconds at each of six randomly chosen locations. Biomass caught per unit effort (BPUE) (g ww·net^{-1}·h^{-1}) was calculated for each annual campaign. BPUE between the years differed significantly (Mann Whitney *U*, Gollinsee: $U_{16} = 64.00$; $p = 0.015$; Schulzensee: $U_{16} = 48.00$; $p = 0.002$), likely due to a severe fish kill that occurred in both lakes as a consequence of a long and cold winter from 2009 to 2010. High abundances of young-of-the-year planktivorous fish occurred in both lakes during 2010, but decreased again in 2011. Biomass was converted to C assuming that dw was 25% of ww (Brey et al. 2010), and that C was 45% of dw (Peters 1983, Wetzel 2001).

To estimate the total fish biomass of each lake in 2010, we applied the detailed biomass estimates from 2011, adjusting for the proportional differences observed in standardized sampling campaigns between years. Fish abundance was estimated in October, 2011 using a mark-recapture approach. During five consecutive days, fish were caught using an electrofishing device, anesthetized with clove oil, and measured. Weight was estimated using our own length-mass regression. Coded wire tags (Northwest Marine Technology, Inc., USA) were inserted into the snout region to tag the fish. After the first day of tagging, all caught fish were visually inspected for tags and further checked using magnetic detectors. Recaptured fish were recorded. To estimate population abundances, we used a Schnabel multiple-census approach, adjusted by Chapman (Ricker 1975):

$$N = \left[\sum (C_t \times M_t)\right] / R + 1 \tag{3}$$

where N is the estimate of the total population abundance, C_t is the number of fish captured during time t, M_t is the number of marked fish captured during time t and R is the total number of fish recaptured during the same period. We used a Poisson variable for 95% confidence limits of abundance estimates, as listed in Ricker (1975).

To obtain fish biomass (g ww·$lake^{-1}$), we multiplied abundances with the geometric mean of the wet weight of all fish tagged. Rough estimates were applied for the biomass of scarce hybrid species, whose low numbers did not allow for an abundance estimate from mark-recapture techniques. Similarly, it was not possible to obtain mark-recapture abundance estimates for sunbleak (*Leucaspius delineatus*, Heckel), as the small body size of this fish species made tagging impossible. We therefore applied the proportion of biomass associated with sunbleak from the total biomass measured from prior samplings. All statistical tests were made using the computer program JMP (Version 7, SAS Institute).

RESULTS

Sedimentation

In phytoplankton-dominated Gollinsee, a constant rate of supply (CRS) model from ^{210}Pb dating provided total C burial rates at the earliest dated segments (roughly 1860 to 1960) which were relatively stable (~50 g C·m^{-2}·yr^{-1}). C burial rates gradually increased over a period dated from roughly 1960 to 2000, after which they appeared to be again relatively stable (mean = 196 g C·m^{-2}·yr^{-1}). During this period, Gollinsee experienced a roughly four-fold increase in

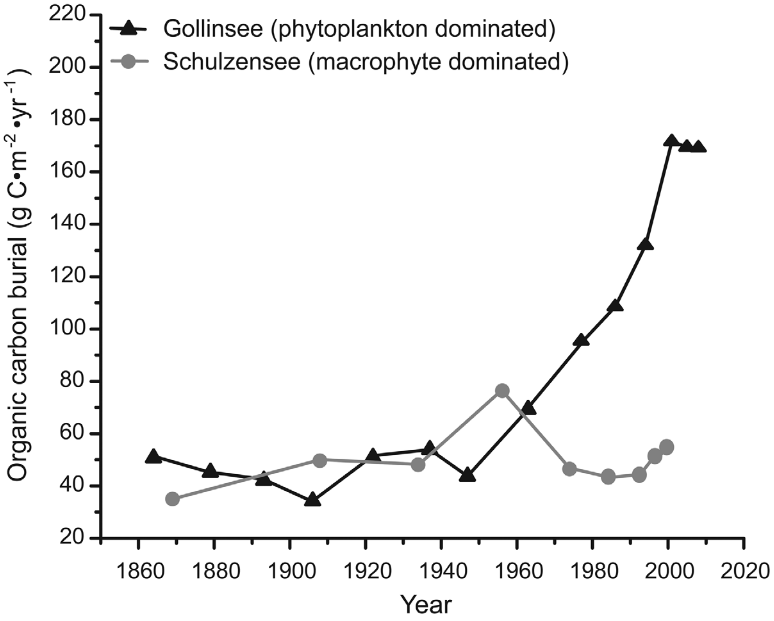

Fig. 2. Historic changes in organic carbon burial rates in phytoplankton-dominated Gollinsee and macrophyte-dominated Schulzensee, determined from CRS models from dated sediment cores.

organic C burial (Fig. 2) and a seven- to eight-fold increase in inorganic C burial. The increase in inorganic C burial appears to be associated almost entirely with a seven-fold increase in calcium carbonate ($CaCO_3$) burial over the same period. Macrofossil analyses identified high concentrations of the oospores of *Characeae* sp. (submerged macrophytes typically associated with clear-water conditions) in sediments dated as recently as 1977, followed by lower concentrations in more recent sediments (data not shown). Leaf fossils from *Potamogeton* sp. (another submerged macrophyte species) were also found in deeper layers (most recently ca. 1900), indicating a possible earlier diversity of submerged macrophytes in this lake. Submerged macrophytes are no longer found in this lake. The dated period when sedimentation rates began to rise (~1960) coincided with a single layer of high sediment loading, and the construction period of a nearby military airport (out of operation since 1990). Together, these factors strongly suggest that the period of increasing sedimentation rates from 1960 to 2000 corresponds to a shift from a macrophyte-dominated to a phytoplankton-dominated regime, resulting from a disturbance associated with nearby anthropogenic activities.

In macrophyte-dominated Schulzensee, a CRS model from ^{210}Pb dating provided C burial rates that did not follow any particular or sustained pattern across the dated segment of the sediment core, and sediments of the top 10 cm were poorly consolidated. Organic C (Fig. 2) and $CaCO_3$ burial rates are roughly equivalent between early (before ~1930) and more recent (~2000) dated periods. Our current estimates of C burial rates in Schulzensee were thus calculated as the mean C burial rate across the full core, excluding a short peak dating to the 1950s as well as the recent (post-2000) poorly consolidated sediments. This provided a mean C burial rate of 53 g $C \cdot m^{-2} \cdot yr^{-1}$, which is roughly equivalent to the pre-shift C burial rates calculated for Gollinsee (~ 50 g $C \cdot m^{-2} \cdot yr^{-1}$).

Comparing total sediment burial rates between both lakes for the layer dating nearest 2000 indicated recent total sediment burial rates of approximately 673 $g \cdot m^{-2} \cdot yr^{-1}$ in Gollinsee and approximately 220 $g \cdot m^{-2} \cdot yr^{-1}$ in Schulzensee. Although there thus appeared to be a large difference between lakes in terms of permanent C and sediment burial rates, sediment deposition rates measured by sediment traps did not differ between lakes (Gollinsee = 681 ± 130 $g \cdot m^{-2} \cdot yr^{-1}$, Schulzensee = 708 ± 140 $g \cdot m^{-2} \cdot yr^{-1}$; *t*-test, $p = 0.89$). The C fraction of freshly deposited sediments, however, was significantly higher in macrophyte-dominated Schulzensee (mean = 37 ± 1%) than in phytoplankton-dominated Gollinsee (28 ± 1%) (*t*-test, $p < 0.0001$). Mean calculated C deposition rates were therefore somewhat higher in Schulzensee (285 ± 65 $C \cdot m^{-2} \cdot yr^{-1}$) than Gollinsee (191 ± 63 g $C \cdot m^{-2} \cdot yr^{-1}$), although the difference between lakes was not statistically significant (*t*-test, $p = 0.30$).

Dividing sediment burial values by our measured sediment deposition rates (from sediment traps) suggests that the sediment burial efficiency in Gollinsee is nearly 100%, but only approximately 30% in Schulzensee. Dividing C burial rates (Gollinsee = 196 g $C \cdot m^{-2} \cdot yr^{-1}$, Schulzensee = 53 g $C \cdot m^{-2} \cdot yr^{-1}$, from dated sediment cores) by C deposition rates, and estimating a range of error from the mean fraction of the standard deviation to the mean of replicate sediment traps, provides C burial efficiency estimates of 102 ± 14% in Gollinsee compared to 19 ± 30% in Schulzensee.

As dating errors are difficult to quantify due to possible fluctuations in ^{210}Pb inputs, historic sediment mixing, and ^{210}Pb diffusion in the upper sediments, we do not present specific errors, but instead note that the degree of uncertainty in dating increases exponentially in deeper sediment layers, and suggest error ranges (with a 95% confidence interval) of 10 to 20 years within the past dated 100 years, following Binford (1990). The accuracy of sediment core dating was, however, validated by measuring ^{137}Cs (which typically peaks at 1963, the year of the nuclear Test Ban Treaty signing) as an independent tracer (e.g., Appleby 2001). In Gollinsee, the peak ^{137}Cs input was identified at a depth of 30–31 cm, which corresponded to a CRS model extrapolated depth of 30.5 cm for 1963. In Schulzensee, the peak ^{137}Cs input was identified at 28–29 cm, which correctly fell between CRS modeled depths for 1956 (31–32 cm deep) and 1974 (24–25 cm deep). Due to the close correspondence between ^{210}Pb and ^{137}Cs approaches in both lakes, we suggest that these sediment chronologies may be considered reliable.

Carbon balances

Measured lake parameters in each system are provided in Table 1. Allochthonous C loading into both lakes was dominated by emergent macrophytes (Fig. 3), though their input was calculated to be nearly three times greater in phytoplankton-dominated Gollinsee than in macrophyte-dominated Schulzensee (Table 2), due to higher reed densities (184 culms/m^2 in Gollinsee, 45 culms/m^2 in Schulzensee). Mean groundwater DOC concentrations were 7.4 ± 1.6 mg/L in Gollinsee and 7.3 ± 1.9 mg/L in Schulzensee, and mean groundwater DIC concentrations of 41.4 ± 2.3 mg/L in Gollinsee and 40.4 ± 2.6 mg/L in Schulzensee. Although total resulting groundwater gains and losses of DOC and DIC were minor relative to other inputs, our data indicated that both lakes received a net gain of groundwater carbon (Table 2).

Both lakes were expected to be net heterotrophic (ER > GPP) as they were both generally supersaturated with pCO_2 (following Cole et al., 1994), yet full-year CO_2 emissions were highest in macrophyte-dominated Schulzensee (Table 2). Pelagic pCO_2 concentrations (derived from DIC concentrations) were also significantly higher in Schulzensee (5.5 ± 0.6 g CO_2/m^3, $n = 20$) than in phytoplankton-dominated Gollinsee (2.8 ± 0.6 g CO_2/m^3, $n = 20$, *t*-test, $p = 0.002$), with chemical enhancement increasing estimated annual fluxes by approximately 30% in both systems. Although the groundwater DIC represented a larger proportion of the loaded C in Schulzensee (Fig. 3), similar groundwater DIC concentrations and net loading rates (Table 2) between these lakes suggest that the significant difference observed in pelagic DIC concentrations (and surface emissions) is most likely due to within-lake metabolic processes, rather than differences in hydrology (Stets et al. 2009) or catchment productivity (Maberly et al. 2012).

Our C mass balances approached equilibrium for each lake, indicating that the major processes described may be reasonably well defined (Table 2). Our C balances show that, of the current annual C losses in phytoplankton-dominated Gollinsee, approximately 82% is permanently buried and 16% is emitted to the atmosphere (the remainder is lost via groundwater transport). Of the current annual C losses in macrophyte-dominated Schulzensee, 34% appears to be

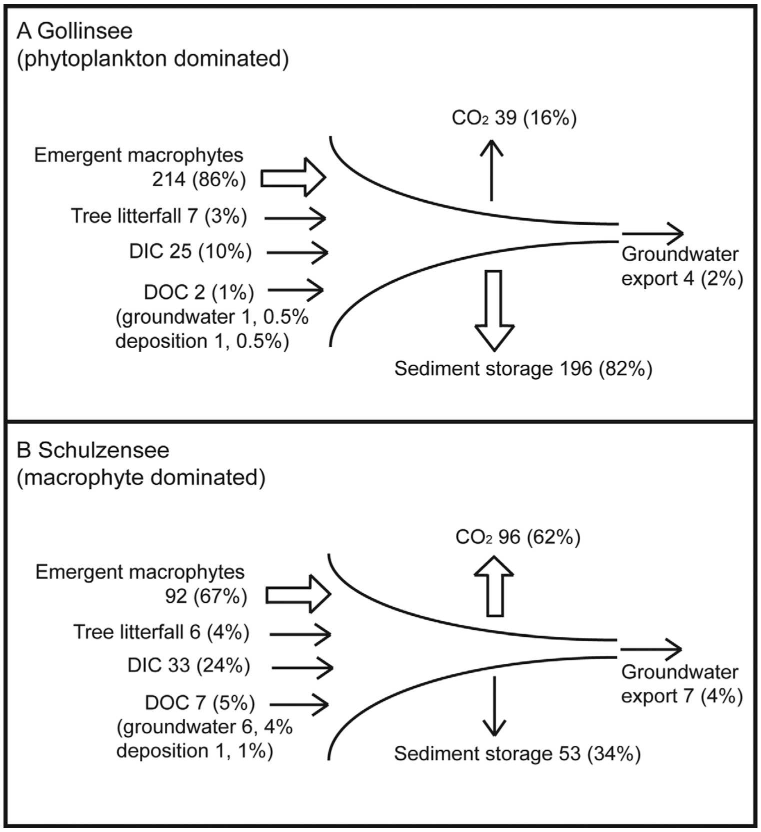

Fig. 3. Synthesis of C flux estimates in (A) Gollinsee and (B) Schulzensee, from mass balances (adapted from Tranvik et al. 2009). Absolute values provided in g C·m^{-2}·yr^{-1}. "Emergent macrophytes" here includes emergent and floating-leaved macrophytes.

Table 2. Full-year carbon gains and losses in study lakes (g C·m^{-2}·yr^{-1}): phytoplankton-dominated Gollinsee and macrophyte-dominated Schulzensee.

Factor	Carbon budget applied	Gollinsee In	Gollinsee Out	Schulzensee In	Schulzensee Out
$DOC_{groundwater}$	E, M	1	1	6	1
$DIC_{groundwater}$	M	25	3	33	6
DOC_{wet}‡	E, M	1	...	1	...
OC_{litter}	E, M	7	...	6	...
OC_{mac}	E, M	214	...	92	...
C_{photo}§	E	...	13	...	13
$C_{emission}$	M	...	39	...	96
C_{sed}	E, M	...	196	...	53
Gross primary production	E	408†	...	586†	...
Ecosystem respiration	E	...	524	...	559
Ecosystem budget	E	631	734	691	626
Mass balance	M	248	239	138	156

Note: Carbon budget approaches are: E, ecosystem budget; M, mass balance.
† From Brothers et al. (2013).
‡ From Andersson and Sobek (2006).
§ From Granéli et al. (1996).

Table 3. Production and respiration estimates for 2010–2011 for the study lakes: phytoplankton-dominated Gollinsee and macrophyte-dominated Schulzensee.

	Gollinsee			Schulzensee		
Producer group	Biomass (mg C/m^2)	Gross production (g C·m^{-2}·yr^{-1})	Respiration (g C·m^{-2}·yr^{-1})	Biomass (mg C/m^2)	Gross production (g C·m^{-2}·yr^{-1})	Respiration (g C·m^{-2}·yr^{-1})
Aquatic plants†	...	408	144	...	586	214
Sediment bacteria	...	440	308	...	352	246
Biofilm bacteria	...	2	2	...	17	12
Pelagic bacteria	...	34	24	...	29	20
Zooplankton	582	...	22	635	...	24
Macro-invertebrates	704	...	8	2464	...	27
Fish	1339	...	16	1336	...	16
Total	...	...	524	...	...	559

† From Brothers et al. (2013).

permanently buried in the sediments, and 62% is emitted to the atmosphere (Fig. 3). Calculated ER rates were similar between systems, with the majority of respiration allocated to sediment bacteria (50–60%) and plants (20–30%; Table 3). Ecosystem C budgets of both lakes were imbalanced by approximately 15%, likely due to the imprecision of our estimates of plant and bacterial respiration rates (see *Discussion: Benthic mineralization*).

DISCUSSION

Burial efficiency

Our data illustrate that regime shifts from macrophyte to phytoplankton dominance in shallow lakes may be linked to a major increase in C burial efficiency. Specifically, our data suggest that nearly all deposited C in phytoplankton-dominated Gollinsee was annually buried in the sediments, compared to only 20% in the macrophyte-dominated Schulzensee. This difference in C burial efficiency suggests that C reaching the sediments in Gollinsee is less likely to return to the aquatic environment, a conclusion which is supported by the lower pelagic DIC concentrations and surface emission rates in Gollinsee.

Summertime sediment O_2 demands (here converted to C assuming a respiratory quotient of one) support our hypothesis of higher benthic C mineralization rates in Schulzensee (mean = 168 ± 33 g C·m^{-2}·yr^{-1}, $n = 14$) than in Gollinsee (mean = 73 ± 23 g C·m^{-2}·yr^{-1}, $n = 30$, t-test, $p = 0.02$; K. Attermeyer and S. Meyer, *unpublished data*). These data further show that some deposited C in Gollinsee is mineralized at the sediment surface and not immediately buried. This suggests that an annual C burial efficiency approaching 100% in Gollinsee may be the result of a more complex process whereby DIC released from the sediments has a greater chance of being incorporated into phytoplankton or calcite and returned to the sediments, rather than being transmitted directly to the atmosphere. A seven-fold increase in calcite burial in Gollinsee from 1960 to 2000 indicates that calcite precipitation, frequently associated with high pH values and a lower ecosystem heterotrophy (Kalff 2002:222–225), may have played such a role. In the most recent (top) sediment layers, inorganic C associated with calcite only represents a small proportion (under 5%) of the total C mass buried, yet $CaCO_3$ altogether represents roughly 30% of the total sediment burial. The influence of calcite on deposition (and thus total sedimentation) rates may in fact be higher than this, as calcite crystals frequently produce detritus aggregates which also increase the sedimentation of other nutrients and organic matter (Kalff 2002:222–225). Net groundwater inflow rates and Ca concentration measurements (calculated from all available data from 2010 to 2012 to minimize any error from annual variability in weather and groundwater loading) provided annual Ca groundwater input rates of approximately 60 g Ca·m^{-2}·yr^{-1} for both lakes. In Gollinsee, this was equivalent to the calculated Ca burial rate in the most recent dated sediment layer. In Schulzensee, recent Ca burial rates were closer to 20 g Ca·m^{-2}·yr^{-1}. This suggests that calcite precipitation in these lakes is feasible at the rates observed in the sediment records, and that the difference in calcite precipitation rates between lakes does not appear to be due to differences in loading rates, but is instead likely due to differences in pH.

Following Brothers et al. (2013), we expected that the recent loss of a submerged macrophyte community in Gollinsee likely resulted in a net decrease in GPP which contributed to the currently lower GPP rates in Gollinsee than Schulzensee. The largest calculated source of allochthonous C to Gollinsee was the shoreline reed community, which is not expected to have increased significantly over the observed period of rising C burial rates, especially since eutrophic conditions tend to have a negative impact on reed communities (van der Putten 1997). Comparing our study lakes, a regime shift-mediated increase in C burial efficiency thus appears to provide a more likely explanation for the historic increase in C burial rates in Gollinsee than an increase in watershed C loading (which was quantified, and small due to the lack of surface in- and outflows) or nutrients (which did not differ significantly between systems).

Benthic mineralization

The high C burial efficiency in Gollinsee is influenced by the apparently reduced C mineralization rates in the sediments. In addition to the sediment O_2 demand measurements, hypolimnetic O_2 concentrations provide another independent measure of sediment respiration which indicates lower sediment mineralization rates in Gollinsee than Schulzensee. Although both lakes were shallow, their sheltered position decreased wind exposure enough to regularly allow for a vertical O_2 concentration gradient. During a relatively strong and stable period of stratification in July 2010, hypolimnetic O_2 concentrations in phytoplankton-dominated Gollinsee decreased at a rate of 2.6 mg $O_2 \cdot m^{-2} \cdot d^{-1}$. This corresponds to a (hypolimnetic) net ecosystem production rate (NEP; GPP − ER) of −0.4 g $C \cdot m^{-2} \cdot yr^{-1}$, applying a respiratory quotient of one. During the same month, hypolimnetic O_2 concentrations in macrophyte-dominated Schulzensee decreased at a rate of 123 mg $O_2 \cdot m^{-2} \cdot d^{-1}$ (corresponding to a NEP of −17 $C \cdot m^{-2} \cdot yr^{-1}$). As these rates represent the difference between GPP and ER, the difference in benthic respiration rates between the lakes may be higher than these data suggest as benthic primary production would likely have benefited from the greater water clarity in Schulzensee ($Z_{secchi} = 2.0–2.2$ m) over Gollinsee ($Z_{secchi} = 1.2–1.5$ m) during this period. Estimated ER rates were similar between these lakes, yet both our direct measurements of benthic metabolism and the imbalance of our ecosystem budgets suggest that true ER rates are likely higher than those calculated for Schulzensee and lower in Gollinsee.

Our higher measured C burial efficiency in macrophyte-dominated Schulzensee is furthermore in agreement with Sobek et al. (2009), who observed a strong negative relationship between O_2 exposure time and organic C burial efficiency across 27 study lakes. Although mixing events and seasonal benthic primary productivity in our systems resulted in full-year hypolimnetic O_2 concentrations which did not differ significantly between lakes (Gollinsee mean = 33 ± 8%, Schulzensee mean = 27 ± 8%, $n = 16$; t-test, $p = 0.6$), profiles taken during the summer months alone measured significantly higher benthic O_2 saturation in Schulzensee (37 ± 10%) than in Gollinsee (9 ± 8%; Table 1). With seasonally lower hypolimnetic O_2 concentrations, the likelihood of anoxia at the sediment level would increase, with potentially negative consequences to secondary benthic communities. Cole and Pace (1995) show that anoxic conditions lead to higher abundances of sediment bacteria, but a slower doubling time. It is suggested that this could lead to higher rates of organic matter preservation, which would be consistent with our own findings. A greater summertime O_2 supply rate to the sediments in Schulzensee due to higher epipelon production rates could have therefore contributed to the lower observed C burial rates in this macrophyte-dominated lake. The darker conditions or the benthic instability in phytoplankton-dominated lakes such as Gollinsee would likely decrease the epipelon productivity in such systems (Kufel and Ozimek 1994, Vermaat et al. 2000, Genkai-Kato et al. 2012).

Concerning the mechanism behind differences in benthic C mineralization in these study lakes, our ecosystem budgets indicated that sediment bacteria were the dominant source of respiration in both lakes (Table 3). Although we observed a higher benthic O_2 demand and generally more heterotrophic conditions (lower pH and higher DIC concentrations) in macrophyte-dominated Schulzensee, it appears somewhat counter-intuitive that measured sediment bacterial production was highest in phytoplankton-dominated Gollinsee (Table 3). This is not necessarily surprising, however, as our application of a common bacterial growth efficiency (BGE) value of 30% provides only a rough, first-order estimate of the bacterial contribution to whole-lake respiration rates. A positive relationship observed between bacterial production and BGE (del Giorgio and Cole 1998) may have provided Schulzensee with a lower BGE (resulting in a proportionally higher release of DIC to the aquatic environment). Other factors influencing BGE (such as nutrient concentrations) have been identified by del Giorgio and Cole (1998), but did not differ significantly between these systems. There is evidence to suggest that a diminished exposure to light may increase the BGE of bacterial communities (e.g., Pullin et al. 2004) providing another mechanism whereby a phytoplankton-dominated regime may be associated with a higher BGE (and thus C burial efficiency). Finally, we note that our estimates of bacterial production were made from the top sediment layer, and that bacterial metabolism may be substantial at deeper layers (Graf 1987, Rothfuss et al. 1997). As we did not measure bacterial production below the surface sediments, we cannot rule out that bacterial production or growth efficiency in deeper layers may differ between these lakes.

Lake morphology has been found to play an important role in explaining large-scale patterns in sediment respiration rates (den Heyer and Kalff 1998) and C burial rates (Ferland et al. 2012). Other studies of large-scale patterns in C burial have however focused on lakes which tend to be one or more orders of magnitude larger than those included in this study (e.g., Heathcote and Downing 2012). A model based on data from our study lakes found that the relationship observed between regime shifts and primary productivity would likely only apply to shallow lakes at moderate nutrient concentrations and with mean depths below 3 or 4 m (Brothers et al. 2013). This suggests that higher C burial rates with regime shifts to phytoplankton dominance in deeper or more eutrophic systems may indeed result from increasing phytoplankton (and thus whole-lake) GPP rates (Heathcote and Downing 2012). Larger scale and broader term studies will be needed to confirm these findings. Nevertheless, our conclusions may be considered widely relevant, as lakes that are equal or smaller than those studied here (ca. 0.03 km^2) represent a large fraction of the world's lakes, comprising roughly 30% of the world's lake surface area (Downing et al. 2006). For such shallow aquatic systems, we suggest that future research should consider the possible effects of the loss of a submerged macrophyte community alongside other established factors which have been shown to strongly influence C burial rates, such as watershed erosion and nutrient loading (Heathcote and Downing 2012, Theissen et al. 2012, Heathcote et al. 2013).

Conclusions

The higher C burial rates detected in our phytoplankton-dominated study lake compared to a similar lake featuring macrophyte dominance are due to a high C burial efficiency. This is apparently the result of diminished benthic C mineralization rates coupled with higher rates of calcite precipitation and burial, both associated with a lowered heterotrophy. In contrast to previous studies on larger systems, we identify increasing historic C burial rates despite an apparent decrease in whole-lake GPP, and no expected shift in allochthonous carbon loading (given the relatively closed nature of both lakes, and the results of our C mass balances). We therefore suggest that a regime shift involving the loss of submerged macrophytes may lead to a decline in ecosystem heterotrophy by lowering C mineralization rates, producing equivalent net metabolic shifts and C cycling results in these shallow lakes to those observed in larger systems by other mechanisms.

Cole et al. (2007) describe a generalized C cycling role for lakes as channels of terrestrial C to the atmosphere, yet our study suggests that a regime shift involving the loss of submerged macrophytes in shallow lakes could alter this role. With decreasing C mineralization rates under phytoplankton dominance, the fraction of an allochthonous C load annually transmitted to the atmosphere declines, and a higher fraction of this C is permanently buried. As regime shifts become increasingly widespread across numerous ecosystem types (Barnosky et al. 2012), it is important to consider how these changes will influence the patterns of C transport throughout the biosphere.

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