Plant community structure determines primary productivity in shallow, eutrophic lakes

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Running head: Community structure determines primary production

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Summary

1. Regime shifts are commonly associated with the loss of submerged macrophytes in shallow lakes, yet the effects of this on whole-lake primary productivity remain poorly understood. This study compares the annual gross primary production (GPP) of two shallow, eutrophic lakes with different plant community structures but similar nutrient concentrations.

2. Daily GPP rates were substantially higher in the lake containing submerged macrophytes (586 ± 23 g C m⁻² y⁻¹) than in the lake featuring only phytoplankton and periphyton (408 ± 23 g C m⁻² y⁻¹; P < 0.0001). Comparing lake-centre diel oxygen curves to compartmental estimates of GPP confirmed that single-site oxygen curves may provide unreliable estimates of whole-lake GPP. The discrepancy between approaches was greatest in the macrophyte-dominated lake during the summer, with a high proportion of GPP occurring in the littoral zone.

3. Our empirical results were used to construct a simple conceptual model relating GPP to nutrient availability for these alternative ecological regimes. This model predicted that lakes featuring submerged macrophytes may commonly support higher rates of GPP than phytoplankton-dominated lakes, but only within a moderate range of nutrient availability (total phosphorus ranging from 30 to 100 μg L⁻¹) and with mean lake depths shallower than 3 or 4 m.

4. We conclude that shallow lakes with a submerged macrophyte-epiphyton complex may frequently support a higher annual primary production than comparable lakes that contain only phytoplankton and periphyton. We thus suggest that a regime shift involving the loss
of submerged macrophytes may decrease the primary productivity of many lakes, with potential consequences for the entire food webs of these ecosystems.

**Introduction**

Primary production supplies aquatic ecosystems with a direct, local food source, and thus represents a fundamental component of the food web of a lake. In shallow aquatic systems, primary production is frequently provided by phytoplankton, periphyton and submerged macrophytes. The relative contribution of each group to gross primary production (GPP) typically varies according to nutrient and light availability (e.g. Vadeboncoeur, Lodge & Carpenter, 2001). It has long been accepted that a positive relationship exists between nutrient concentrations and primary production in lakes, driven predominantly by phytoplankton dynamics (e.g. Smith, 1979). Increasingly, studies have reassessed whether this generalization applies to whole-lake primary productivity, because it may ignore the effect of decreasing periphyton production due to light limitation by elevated phytoplankton concentrations (Vadeboncoeur et al., 2001; Vadeboncoeur, Vander Zanden & Lodge, 2002; Blindow et al., 2006). This shading effect is especially important in small lakes (surface area < 2.5 km²), which represent approximately 99% of all lakes (Downing et al., 2006), and whose benthic zones are often shallow enough to support a major share of the lake’s total primary productivity (Vadeboncoeur et al., 2002, 2008).

It is currently understood that ecological responses to eutrophication and/or habitat disturbances are not necessarily gradual, but are instead often typified by rapid shifts between alternative stable regimes (e.g. Folke et al., 2004). Regime shifts in
temperate-zone, shallow lakes frequently occur between a clear-water regime featuring submerged macrophytes and a turbid regime of phytoplankton dominance (Scheffer *et al.*, 1993a). Either regime may exist at an intermediate range of nutrient loading, and shifts may be triggered by changes in nutrient loading or by stochastic perturbations such as food-web alterations (e.g. Jeppesen *et al.*, 1990) or extreme weather events (Scheffer *et al.*, 1993a, 2001). Submerged macrophyte communities can play an important ecosystem function by increasing the available surface area for epiphyton production, while positively influencing the light climate by reducing phytoplankton abundance through a variety of mechanisms (Scheffer *et al.*, 1993a; Hilt & Gross, 2008). It is thus feasible that a regime shift resulting in the loss of a submerged macrophyte-epiphyton complex may lead to major changes in a lake’s food-web structure and productivity independently of ambient nutrient concentrations.

Few studies have addressed quantitatively the impact of plant community structure on whole-lake primary production. Previous studies in shallow lakes have suggested that a clear-water regime with submerged macrophytes may support either less (Mitchell, 1989) or more (Blindow *et al.*, 2006) net primary production (NPP) than a turbid, phytoplankton-dominated regime. Such results cannot be readily compared, however, since primary production of periphyton is often overlooked (e.g. Mitchell, 1989; Vadeboncoeur *et al.*, 2002). Furthermore, a tendency to compare lakes with broadly different nutrient concentrations does not allow for a clear analysis of the role of plant community structure alone. The present study aims to avoid this complication by comparing the full annual GPP of two shallow lakes that exhibit alternative plant community structures at similar nutrient concentrations. Our study focuses specifically on
GPP (instead of NPP) following previous research (e.g. Liboriussen & Jeppesen, 2003), and providing data suitable for future analyses of the specific role of primary producers in the lake carbon cycle.

We hypothesized that the annual whole-lake GPP of a shallow lake featuring a submerged macrophyte-epiphyton community would be greater than a phytoplankton-dominated system with similar nutrient concentrations. We expected that this difference would be due to the additional productivity of the submerged macrophyte-epiphyton complex, as well as higher rates of epipelon production resulting from a greater benthic light availability in the lake containing submerged macrophytes. As the spatial distribution of primary production in lakes is often highly heterogeneous (e.g. Van de Bogert et al., 2012; Staehr et al., 2012), we adopted two independent and parallel approaches to quantify the differences in whole-lake GPP between study lakes. In order to broaden the applicability of our results to other systems, we aimed to use our empirical data to construct a simple conceptual model to predict the whole-lake GPP of lakes with and without submerged macrophytes across a broader gradient of total phosphorus (TP) concentrations.

Methods

Study sites

Kleiner Gollinsee (53°01’N, 13°35’E, hereafter referred to as Gollinsee) and Schulzensee (53°14’N, 13°16’E) are small, shallow, eutrophic lakes (Table 1) located in a moderately low-lying rural area of northeastern Germany (approximately 100 km north of Berlin). Schulzensee contains non-rooted submerged macrophytes (primarily Ceratophyllum
submersum) and colony-forming cyanobacteria (Aphanothece stagnina), and features a slightly greater water clarity than Gollinsee at similar nutrient concentrations (Table 1). The only aquatic primary producers in Gollinsee are phytoplankton and periphyton (attached algae that grow as epiphyton on macrophyte surfaces or as epipelon on muddy sediments). Neither lake features surface inflows or outflows, and both lakes are naturally sheltered, and thus expected to experience only minor wind-driven resuspension. Both lakes are in forested catchments, and are completely encircled by alder trees (Alnus glutinosa) and a reed belt (Phragmites australis), with some stands of floating-leaved plants (Nymphaea alba, Nuphar lutea). Although the lake surface area occupied by submerged macrophytes is relatively small (20-25%), we here refer to Schulzenensee as macrophyte dominated, following Hilt & Gross (2008) who suggest that this coverage is high enough to influence phytoplankton production, and thus water clarity. A comparison of Secchi disk readings, DOC concentrations and chlorophyll a (chl a) concentrations indicated that transparency in our study lakes was much more strongly predicted by phytoplankton chl a concentrations (t-test; $r^2 = 0.37$, $P < 0.001$) than DOC ($r^2 = 0.005$, $P = 0.79$). This suggests that these lakes are appropriate for a study of biological controls that influence the dominance of different plant groups and whole-lake GPP. As phytoplankton was the primary biotic determinant of water clarity and thus GPP of other primary producers in Gollinsee, we here refer to this lake as phytoplankton dominated.

General sampling and analysis

Pelagic water samples (containing equal parts water from 0.5 m, 1 m, and 2 m at the lake centre) and littoral samples (mixing sub-surface water equally from three random
locations within the reed belt) were taken every two to four weeks from early April 2010 to early April 2011. While littoral samples were always taken from within the reed belt, we define the littoral zone as any lake area with macrophytes (submerged, floating-leaved or emergent). As the lake area coverage of *C. submersum* overlapped with, and was larger than that of floating-leaved macrophytes (Table 2), only emergent (reeds) and submerged macrophyte surface areas were used to calculate the total littoral area in Schulzensee (Table 1). Measurements of concentrations of TP, soluble reactive phosphorus (SRP), total nitrogen (TN), dissolved nitrogen (DN) and dissolved organic carbon (DOC) were made separately for the littoral and pelagic zones. Chemical analyses were carried out following standard laboratory procedures (DEV, 2009).

Monthly vertical profiles of pelagic oxygen (O₂), temperature and pH were measured from the water surface to the sediment at 50 cm intervals using a Yellow Springs Instruments (YSI, Xylem Inc., Yellow Springs, OH, USA) monitoring probe. YSI probes were also installed at lake-centre monitoring stations (from early May) at a depth of approximately 1.2 m (varying with lake level fluxes). These probes recorded temperature, O₂, and pH every 10 minutes during the study year. Light attenuation was measured across the water column from simultaneous light intensity values recorded by two Underwater Spherical Quantum Sensors (LI-193, LI-COR) fixed vertically 50 cm apart. Secchi disk readings were used to estimate light attenuation on dates when direct measurements were unavailable or unreliable. Lake-centre monitoring stations measured global radiation every 10 minutes. Global radiation data from Lake Müggelsee (approximately 100 km to the south) were substituted when data were missing from either study lake. Photosynthetically active radiation (PAR) at depth z (I₁) was calculated from
light attenuation and global radiation (1 W m$^{-2}$ of global radiation being equivalent to a PAR of 2.12 µmol m$^{-2}$ s$^{-1}$) using the equation:

$$I_z = I_0 \cdot e^{-\varepsilon \cdot z} \quad (1)$$

where $I_0$ represents the mean surface irradiance and $\varepsilon$ represents light attenuation.

**Macrophytes**

The areal limit of each macrophyte group was measured in 2007 by direct measurements, and in 2010 using a global positioning system (GPS). The direct exchange of carbon dioxide (CO$_2$) and O$_2$ between the aquatic environment and the submerged segments of floating-leaved or emergent macrophytes was expected to be minimal (Brix & Schierup, 1990; Smits et al., 1990). We therefore included only the submerged macrophyte *C. submersum* in GPP calculations. The plant volume inhabited by *C. submersum* (PVI) was determined by measuring the water depth limits of occurrence at 24 points around the lake periphery during the period of maximum biomass (July 2010).

Fixed-volume biomass samples were harvested from four locations and dried at 80 °C to a constant dry weight (dw). The maximum *C. submersum* biomass was calculated by multiplying PVI by dw m$^{-3}$ and was converted to carbon using total carbon values measured with a vario EL CHNOS Element Analyzer (Elementar Analysensysteme, Hanau). GPP was calculated by multiplying the summer biomass by a gross production rate-to-harvest ratio of 1.5, determined by Best (1982) for *C. demersum*
in a shallow lake in the Netherlands, and was estimated for an active growing period of six months of the year (following observations).

Periphyton

The biomass and GPP of periphyton on submerged plastic strips (transparent polypropylene sheets with a slightly textured surface; IBICO, Germany) were considered to be similar to periphyton growing directly on the submerged surfaces of macrophytes (epiphyton) and the benthic surface (epipelon), corrected for a gradient in light availability. This approach has been used previously and is considered valid for eutrophic systems (e.g. Eminson & Moss, 1980; Köhler, Hachoł & Hilt, 2010). Plastic strips were installed in early April 2010 in the open-water and littoral zone of each lake at a depth of 1.2 m, with one end in contact with the sediment to allow access to grazers. Subsamples were harvested monthly during the ice-free period.

Large plastic strips (2 cm x 22 cm) were transported in open plastic cylinders in a humid, insulated box to a laboratory, where they were brushed and washed with filtered lake water to remove periphyton. The remaining solution was filtered to provide chl $a$ concentrations using high-performance liquid chromatography (HPLC, Waters, Millford, MA, USA), following methods in Shatwell, Nicklisch & Köhler (2012). Small plastic strips (1 cm x 5 cm) were transported in sealed tubes filled with filtered lake water, and were used for in vivo absorption and fluorometric laboratory measurements.

Periphyton GPP on the plastic strips was measured using a pulse amplitude modulated fluorometer (Phyto-PAM EDF, Walz, Effeltrich, Germany). The carbon assimilation rate
of primary producers ($C_{\text{assim}}$, g C g chl $a^{-1}$ h$^{-1}$) was calculated from the formula (adapted from Kromkamp & Forster, 2003):

$$C_{\text{assim}} = Y \cdot \text{PAR} \cdot 0.0036 \cdot a^* \cdot E \quad (2)$$

where $Y$ is the quantum yield of photosystem II (PSII), PAR is the intensity of photosynthetically active radiation ($\mu$mol m$^2$ s$^{-1}$), 0.0036 converts $\mu$mol s$^{-1}$ into mol h$^{-1}$, and $a^*$ is the specific absorption of periphyton (m$^2$ g chl $a^{-1}$), calculated as the absorption of photosynthetic pigments (m$^{-1}$, measured by a Varian spectrophotometer) divided by the HPLC-derived chl $a$ concentration (g chl $a$ m$^{-3}$). $E$ is the efficiency of carbon assimilation (0.766 g C mol$^{-1}$), calculated as the slope between the electron transport rates and carbon assimilation rates from $^{14}$C measurements in Lake Müggelsee (J. Köhler, unpubl. data). Kromkamp & Forster (2003) explicitly include the ratio between Photosystems I and II in their productivity calculations, yet here this ratio is contained in $E$. $Y$ was calculated using the formula from Genty, Briantais & Baker (1989):

$$Y = (F_m - F_I) \cdot F_m^{-1} \quad (3)$$

where $F_m$ is the fluorescence induced by saturating light flashes, and $F_I$ is the fluorescence induced by incrementally lower light intensities. As detritus was expected to influence our measurements of the absorption of photosynthetic pigments ($a_p$), these values were corrected using a previously established relationship from Lake Müggelsee ($r^2 = 0.95$, n = 174; J. Köhler, unpubl. data):
\[ a_p = 0.647 \cdot a_{t,676} + 0.527 \cdot a_{t,626} - 0.215 \cdot a_{t,438} + 0.096 \]  \hspace{1cm} (4)

where \( a_{t,\lambda} \) is the measured absorption (m\(^{-1}\)) at wavelength \( \lambda \).

Light-saturated photosynthesis (\( P_{\text{max}} \)) and photosynthetic efficiency at low light (\( \alpha \)) were calculated from rapid light curves by fitting to the model of Eilers & Peeters (1988). Measurements were made at room temperature (24 °C), and thus \( P_{\text{max}} \) rates were corrected to lake temperatures using the relationship determined from Lake Müggelsee (\( r^2 = 0.73, n = 148; J. Köhler, unpubl. data) :

\[ P_{\text{max}T} = P_{\text{max}} \cdot (0.409 + 0.1487 \cdot T) \cdot (0.409 + 0.1487 \cdot 24)^{-1} \]  \hspace{1cm} (5)

where \( T \) is water temperature (°C). An exponential regression of this dataset provides a \( Q_{10} \) value of 1.88, which is comparable to the commonly adopted \( Q_{10} \) of 2 for phytoplankton production (e.g. Gilbert et al., 2000).

Periphyton GPP was calculated by applying the equation of Webb, Newton, & Starr (1974):

\[ P_z = P_{\text{max}} \cdot \text{chl} \cdot a \cdot (1 - e^{(-\alpha \cdot I_z \cdot P_{\text{max}}^{-1})}) \]  \hspace{1cm} (6)

where \( P_z \) is the production at depth \( z \) (μg C L\(^{-1}\) h\(^{-1}\)), considered to be 50% mean macrophyte depth for epiphyton GPP, and mean habitat depth (littoral or open-water) for epipelon GPP. Light availability was provided from hourly global radiation data.
To estimate the surface area available to epiphyton GPP in each lake, direct measurements of stem diameter, mean depth of occurrence and plant density (per m²) were made for *P. australis* and *N. alba*. A maximum available surface area of 427 cm² g⁻¹ was estimated for *C. submersum* (Armstrong, Planas & Prepas, 2003). For daily available surface area estimates a quadratic growth curve was applied, using the total measured surface area as a mid-summer maximum, and measured dead or dormant fractions of *P. australis* (75% in Gollinsee; 48% in Schulzensee) and *C. submersum* (10%) as a winter minimum (considered December 1st to March 31st). A linear relationship was applied between measurements.

Epipelon (benthic periphyton) GPP was calculated from the periphyton grown in the littoral and open-water zones of each lake. As well-established natural benthic periphyton communities were observed in both lakes throughout the year, monthly production measurements were applied to the periphyton biomass of long-exposure plastic strips to calculate annual production curves. Over-wintering (under-ice) strips could only be retrieved from Schulzensee, but minor differences before and after ice cover suggested that long-exposure strips had probably reached maximum biomasses in both lakes.

**Phytoplankton**

Phytoplankton production was estimated from monthly measurements of chl *a*, fluorescence and light attenuation. Mean whole-lake chl *a* concentrations were adopted, calculated as the weighted mean of measured pelagic and littoral chl *a* concentrations according to the percentage each habitat occupied in each lake. Direct spectrophotometer
measurements were carried out, but bleaching to correct for detritus occasionally produced unreliable absorption ($a_p$) values. The minimum normalized fluorescence of dark-adapted phytoplankton at red excitation ($F_{0,658}$) has been found to provide good estimates of $a_p$ for phytoplankton in Lake Müggelsee ($r^2 = 0.90, n = 176$; J. Köhler, unpubl. data), and phytoplankton $a_p$ was thus calculated as:

$$a_p = (0.00150 \cdot F_{0,658} + 0.082) \cdot \text{chl } a^{-1}$$ (7)

where $F_{0,658}$ is measured by a Phyto-PAM fluorometer, and chl $a$ is measured by HPLC (mg m$^{-3}$).

The fluorescence of water samples was measured within three hours of sampling using the modular version of a Phyto-PAM fluorometer equipped with a 10 mm cuvette, and water was filtered for HPLC and C:N analyses. Production calculations from fluorometric measurements followed the same methods described for periphyton. Phytoplankton GPP was calculated for each 10 cm layer of the water column, applying equation 6. Each measurement was multiplied by the estimated water volume at a specific depth, and the sum of these measurements was used to calculate daily whole-lake phytoplankton production.

Cyanobacteria

*A. stagnina* were observed at the littoral sediments and water surface of macrophyte-dominated Schulzensee. The GPP of individual colonies was measured using $O_2$ production data from *in situ* glass bottle incubations and core exposure experiments on
five dates (spring to summer). For core exposures, opaque \((n = 11)\) and clear \((n = 13)\) replicates of sediment cores were installed at the lake’s mean depth for four-hour periods. For glass bottle exposures, single colonies were inserted into 50 mL transparent and opaque glass flasks filled with filtered lake water \((0.7 \mu m)\), and were incubated for four hours at depths of 0 m, 1 m, 2 m and 3 m. Respiration rates were calculated using \(O_2\) curves from opaque cores and bottles, and were subtracted from net production rates in transparent cores and bottles to calculate GPP. Daily GPP rates were calculated following equation 6, as per periphyton production. \(P_{\text{max}}\) and \(\alpha\) values were obtained from the measured relationship between \(O_2\) production and light intensity, and light availability was considered for sediment depths between 1.5 and 3 m, assuming 20% coverage within that zone (following observations). As colonies were observed at both the benthic environment and occasionally the surface waters, the mean of core and glass bottle GPP values was adopted. Daily rates of \(A.\ stagnina\) GPP were calculated for the 80-day period within which experiments were carried out, and mean rates were extended over the entire nine month ice-free period of the year for whole-lake annual GPP calculations.

\textit{Diel oxygen curves}

Daily GPP rates were calculated using diel \(O_2\) curves provided by YSI probes. Gross nighttime respiration was calculated as the mean change in \(O_2\) \((\text{per 10 minutes})\) from dusk until dawn, and was subtracted from net production rates calculated by the same methods for the following day to provide GPP. Although diel \(O_2\) curves were expected to capture some metabolic activity from the benthic and littoral zones, it has been established that this approach is highly spatially sensitive (Van de Bogert \textit{et al.}, 2012),
and we thus here consider that these data probably contain a strong pelagic bias. As with other studies, variations in dissolved oxygen due to physical factors (e.g. water mixing) and a heterogeneous distribution of primary production in the lakes provided occasionally unreliable diel curves (Coloso et al., 2008). These were excluded from our analyses, as the distribution of false negative values was not normally distributed, and thus did not appear to reflect random patterns in water mixing (Staehr et al., 2010).

Diel O$_2$ curves were corrected for atmospheric O$_2$ fluxes following Gelda & Effler (2002), using lake-centre wind speed data recorded every 10 minutes by a meteo multiprobe (ecoTech, Bonn, Germany). Fluxes were further adjusted for periods of stratification, when surface O$_2$ concentrations from profiles differed from values provided by installed probes. As compartmental fluorescence-based calculations of GPP could not be made during the winter ice-cover period, due to the highly variable light climate related to changes in snow and ice thickness (from 1 December 2010 until approximately 15 March 2011), winter O$_2$ curves were applied for the full-year GPP estimates of each lake. Production values are expressed as C using a respiratory quotient of one. Statistical tests were made using JMP (Version 7, SAS Institute).

**Conceptual productivity model**

The data from our study lakes were used to produce a conceptual model describing GPP as a function of total TP availability in the water column associated with alternative plant community structures. For practical purposes, the TP gradient presented may be considered the springtime ambient TP concentration in a lake prior to partitioning by separate primary producer groups. Parameter values are provided in Table 3.
We considered a trade-off between TP assimilation by planktonic ($TP_p$) and benthic ($TP_b = 1 - TP_p$) producers. This approach simplifies the complex interactions between primary producer groups, representing only the outcome of competitive interactions. Hill functions have previously been found to provide suitable descriptions of the feedbacks between phytoplankton and macrophytes (Scheffer, 1990; Scheffer, Bakema & Wortelboer, 1993b). We therefore adopted such an approach, calculating the partitioning of $TP_p$ between phytoplankton and macrophytes as:

$$TP_p = (TP_m - TP_0) \cdot TP^n \cdot (TP^n + k_p^n)^{-1} + TP_0 \quad (8)$$

where $TP_0$ and $TP_m$ represent the initial and maximum phytoplankton shares of the phosphorus pool, respectively. For lakes without submerged macrophytes, these were set to 0.5 and 1 (respectively). For lakes with submerged macrophytes, we considered that a smaller share of TP could be sequestered by phytoplankton, and these values were thus set at 0.2 and 0.9. A common power coefficient of 3 was applied (e.g. Scheffer et al., 1993b; van Nes et al., 2003), and the half-saturation concentration of TP ($k_p$) was set to 14 mg m$^{-3}$ following Behrendt & Opitz (1996).

Phytoplankton biomass (as chl $\alpha$) was described as a function of $TP_p$ by a Droop-type model, following Köhler, Behrendt & Hoeg (2000):

$$chl \alpha = TP_p \cdot (TP_p \cdot q_0/q_{\text{max}} + k_P) \cdot (q_0 \cdot (k_p + TP_p))^{-1} \quad (9)$$

and periphyton biomass (chl $\alpha$) was calculated according to $TP_b$ and light intensity:
The biomass (chl a) of submerged macrophytes was described as:

\[ \text{chl } a = \text{chl}_{\text{max}} \cdot TP_b \cdot (TP_b + k_p)^{-1} \cdot (1 - e^{-\alpha \cdot \text{ISM}/\text{chl}_{\text{max}}}) \quad (13) \]
where chl$_{\text{max}}$ is the maximum biomass of submerged macrophytes (g chl $a$ m$^{-3}$) at light and nutrient saturation and $\alpha$ is the initial slope of the biomass – light model (from Köhler et al., 2010). The surface area available to epiphyton communities was considered to be 427 cm$^2$ g dw$^{-1}$ (mean for C. demersum from Armstrong et al., 2003) and we applied 166 g dw g chl $a$$^{-1}$ (adapted from Pokorný & Rejmánková, 1983 and Osmond et al., 1981). Self-shading by submerged macrophytes ($I_{\text{sm}}$) was calculated following equation 6 in van Nes et al. (2003). Submerged macrophyte GPP was calculated from the modeled biomass of C. submersum following Best (1982).

**Results**

*Lake conditions*

Over the course of the study year, there were no statistically significant differences between study lakes with regards to TP, SRP or TN concentrations (Table 1). One high SRP outlier in Gollinsee was removed from analyses as it could not be explained by natural conditions or methodological error, although this did not alter the statistical significance of SRP differences between our study lakes.

In Gollinsee, the littoral zone consisted of P. australis (15% of the total lake area) and N. alba (3% of the lake area, Table 1). These corresponded to maximum epiphyton-available surface areas of 1400 m$^2$ on P. australis and 1500 m$^2$ on N. alba. In Schulzensee, the littoral zone consisted of P. australis (10% of the lake area), N. alba (12% of the lake area) and C. submersum (22% of the lake area, or 8% of the lake area).
volume, Table 1). These corresponded to maximum epiphyton-available surface areas of 1500 m$^2$ on *P. australis*, 7700 m$^2$ on *N. alba* and 5600 m$^2$ on *C. submersum*.

**Primary production**

Measured periphyton biomasses on long-exposure littoral plastic strips were only slightly higher in macrophyte-dominated Schulzensee (7.6 ± 1.3 μg chl a cm$^{-2}$) than in Gollinsee (5.0 ± 1.3 μg chl a cm$^{-2}$; $n = 3$, $P = 0.23$). Alternatively, long-exposure biomasses on open-water strips were somewhat lower in macrophyte-dominated Schulzensee (5.6 ± 2.6 μg chl a cm$^{-2}$) than in Gollinsee (7.9 ± 2.6 μg chl a cm$^{-2}$; $n = 3$, $P = 0.56$). We thus calculated a significantly higher full-year epiphyton GPP in macrophyte-dominated Schulzensee, but no significant difference in epipelon GPP between lakes (Table 2). Differences in periphyton GPP between lakes were found to be most pronounced during summer months (June to August), when a higher light attenuation in Gollinsee diminished benthic epipelon GPP and a greater littoral surface area in Schulzensee boosted epiphyton production (Fig. 1a). Detritus correction factors provided mean specific absorption values of 19 ± 3 m$^2$ g chl $a^{-1}$ in Gollinsee and 10 ± 3 m$^2$ g chl $a^{-1}$ in Schulzensee, within the range to be expected for algae from the literature (Tilzer, 1983, and references therein).

Measured pelagic chl $a$ concentrations in phytoplankton-dominated Gollinsee (mean = 23 ± 3 μg L$^{-1}$, $n = 21$) were higher than those in macrophyte-dominated Schulzensee (mean = 13 ± 3 μg L$^{-1}$, $n = 19$; $P = 0.02$). Despite this, a higher mean depth in Schulzensee provided 20% higher depth-integrated annual phytoplankton GPP rates in the macrophyte-dominated lake (Table 2), with the difference between systems being
largest during summer months (Fig. 1b). Detritus correction factors for phytoplankton absorption provided mean specific absorption values of $12 \pm 1 \text{ m}^2 \text{ g chl } a^{-1}$ in Gollinsee and $17 \pm 1 \text{ m}^2 \text{ g chl } a^{-1}$ in Schulzensee, which were 20 to 30% lower than measurements without detritus corrections, and similar to literature values (Tilzer, 1983 and references therein).

For *C. submersum*, we measured a maximum biomass of $316 \pm 97 \text{ g dw m}^{-3} (n = 4)$. Together with *A. stagnina*, these primary producers accounted for 8% of the total estimated GPP in Schulzensee (approximately 4% each, values presented in Table 2). The mean GPP of *A. stagnina* was lower in core exposure experiments ($11 \pm 0.3 \text{ g C m}^{-2 \text{ y}^{-1}}$) than glass bottle experiments ($34 \pm 1 \text{ g C m}^{-2 \text{ y}^{-1}}$), which was attributed to the greater amount of light-exposed surface area for floating *A. stagnina* colonies.

Summer GPP measurements from O$_2$ curves (approximately $1.4 \text{ g C m}^{-2 \text{ d}^{-1}}$ in both lakes) were comparable to whole-lake summertime GPP rates independently calculated in phytoplankton-dominated Gollinsee ($1.6 – 1.9 \text{ g C m}^{-2 \text{ d}^{-1}}$, Fig. 2a), but significantly lower than the summertime GPP rates calculated for macrophyte-dominated Schulzensee ($3.6 - 4.4 \text{ g C m}^{-2 \text{ d}^{-1}}$, Fig. 2b). Instead, diel O$_2$ curves in Schulzensee appeared to better represent calculated phytoplankton GPP (Fig. 2b). Winter GPP measured by O$_2$ curves was significantly higher in Schulzensee ($0.9 \pm 0.2 \text{ g C m}^{-2 \text{ d}^{-1}}$) than in Gollinsee ($0.1 \pm 0.2 \text{ g C m}^{-2 \text{ d}^{-1}}$; t-test, $P = 0.004$).

For the ice-free portion of the study year, daily GPP rates were calculated for all plant groups (monthly means presented in Table 4). Whole-lake annual GPP rates were 40% higher in macrophyte-dominated Schulzensee ($586 \pm 23 \text{ g C m}^{-2 \text{ y}^{-1}}$) than in phytoplankton-dominated Gollinsee ($408 \pm 23 \text{ g C m}^{-2 \text{ y}^{-1}}$; Table 4). Most of this
observed difference was due to the contribution of the submerged macrophyte-epiphyton complex and *A. stagnina* in Schulzensee.

*Conceptual productivity model*

Our empirical data were applied to previously established conceptual relationships between TP availability and GPP, illustrating that at moderate TP concentrations and low mean lake depths most GPP may be supplied by either phytoplankton (in lakes without submerged macrophytes) or benthic algae (in lakes with submerged macrophytes) (Fig. 3a). Our model suggests that with increasing TP, macrophyte–dominated lakes would first exhibit reductions in epipelon GPP, then submerged macrophyte and epiphyton GPP, leading eventually to a full phytoplankton dominance of lake GPP (Fig. 3a). Our model thus suggests that a hump-shaped relationship exists between total GPP and TP in macrophyte-dominated, clear-water lakes (Fig. 3b). At intermediate TP concentrations, the GPP of a clear-water regime is thus higher than that of a turbid regime (Fig. 3b), reflecting our empirical results. Due to the important role of benthic GPP, the difference between regimes diminishes as the mean lake depth increases, and disappears completely beyond mean depths of 3 to 4 m (Fig. 3d, 3f). At higher TP concentrations, phytoplankton and periphyton communities dominate, and our model suggests that the response of GPP to further increases in TP concentrations is relatively weak, since periphyton GPP becomes increasingly light limited, and self-shading by phytoplankton restricts increases in areal pelagic GPP.

**Discussion**
Our results demonstrate that a shallow eutrophic lake featuring a submerged macrophyte community supports a higher full-lake annual GPP than a phytoplankton-dominated lake of comparable morphometry and nutrient concentrations. Although nutrients play an important role in broadly limiting or propelling ecosystem productivity, we here show that the relationship between GPP and nutrient status may be discontinuous in bistable systems. Lower whole-lake GPP rates in the phytoplankton-dominated lake were attributed to the lowered water clarity and presence of fewer primary producer groups. Our conclusions are illustrated by a simple model that suggests the presence of a submerged macrophyte-epiphyton complex in a shallow lake improves benthic light availability, and consequently allows for a greater whole-lake GPP than would be expected for a phytoplankton-dominated lake at similar pelagic TP concentrations.

Comparisons of results between methods and literature

The GPP rates in our study lakes were comparable to those from other studies. Pelagic chlorophyll $a$ concentrations were highest in our phytoplankton-dominated lake, but a higher mean depth in macrophyte-dominated Schulzensee provided that lake with a slightly greater areal phytoplankton GPP. Areal phytoplankton GPP rates in our study lakes (140 to 180 g C m$^{-2}$ y$^{-1}$) were similar to literature values at comparable nutrient concentrations (e.g. 200 to 300 g C m$^{-2}$ y$^{-1}$ from del Giorgio & Peters, 1993; 100 to 400 g C m$^{-2}$ y$^{-1}$ from Liboriussen & Jeppesen, 2003). Our estimates of epipelon GPP (~250 g C m$^{-2}$ y$^{-1}$) are also similar to values published in other shallow lakes (500 g C m$^{-2}$ y$^{-1}$ from Vadeboncoeur & Lodge, 1998; 100 to 1700 g C m$^{-2}$ y$^{-1}$ from Üveges et al., 2011).

Whole-lake GPP values in the literature are typically expressed as daily summertime
rates, and were found to range from 1 to 7 g C m\(^{-2}\) d\(^{-1}\). Summertime (June to August) GPP in Gollinsee (1.8 ± 0.2 g C m\(^{-2}\) d\(^{-1}\)) and Schulzensee (3.7 ± 0.2 g C m\(^{-2}\) d\(^{-1}\)) both fell within this range, with rates being significantly higher in macrophyte-dominated Schulzensee (t-test, \(P = 0.005\)).

Van de Bogert \textit{et al.} (2012) describe a high degree of spatial heterogeneity in summertime diel O\(_2\) curves. A lack of agreement between our separate approaches probably reflects this heterogeneity, especially as the discrepancy between methods in our study appears to be greatest in the macrophyte-dominated lake (where the littoral and benthic zones were expected to play a larger role in whole-lake GPP). Furthermore, the difference between approaches was greatest during the summer, when GPP of the submerged macrophyte-epiphyton complex was highest. Diel O\(_2\) curves in macrophyte-dominated Schulzensee aligned well with calculated phytoplankton GPP, suggesting that these O\(_2\) curves essentially measured pelagic processes. In phytoplankton-dominated Gollinsee, O\(_2\) curves more closely resembled whole-lake GPP. We suspect that these differences were probably due to the slightly shallower mean depth of Gollinsee (with the benthic zone positioned slightly nearer to the installed YSI probes), as well as the greater contribution of the littoral zone to whole-lake GPP in Schulzensee. Alternatively, it is possible that O\(_2\) curves in Gollinsee measured phytoplankton GPP, but that areal production estimates, which incorporated mean lake depth, overestimated GPP rates, which could have been lower in deeper water layers due to self-shading.

We note that this study focuses on gross primary production, while others such as Blindow \textit{et al.} (2006) and Mitchell (1989) have instead chosen to measure net primary production (NPP). NPP is important to consider for food-web effects, as it represents the
supply of autochthonous organic carbon available to consumers. Furthermore, differences in GPP do not always translate directly to NPP. For instance, Blindow et al. (2006) observed a lower GPP but higher NPP in a macrophyte-dominated lake compared to a more eutrophic phytoplankton-dominated lake. While the fluorometric approach adopted in this study does not provide estimates of algal respiration, respiration rates could be calculated for *A. stagnina* following the methods adopted for GPP, and applying the measured relationship between respiration (as O$_2$ consumption) and water temperature. This provided mean respiration rates of 36 ± 1 g C m$^{-2}$ y$^{-1}$ for *A. stagnina*. Rough estimates of NPP may also be provided by incorporating empirical biomass and production data into relationships in the literature. For phytoplankton, 40% GPP was considered lost to respiration (Platt, Bird & Sathyendranath, 1991) though higher losses may be possible (Blindow *et al.*., 2006). A maximum respiration rate of 60% GPP was considered for *C. submersum* (Best, 1982 and references therein). Rough estimates of periphyton respiration rates were calculated using the results of Liboriussen and Jeppesen (2006), who present a relationship between periphyton biomass and respiration rates on summer (July) and autumn (September) plastic strip exposures. Altogether, these corrections provide mean NPP rates of 372 g C m$^{-2}$ y$^{-1}$ in macrophyte-dominated Schulzensee and 264 g C m$^{-2}$ y$^{-1}$ in phytoplankton-dominated Gollinsee. Our conclusions regarding the relationship between GPP and plant community structure thus appear to hold true when considering NPP at intermediate nutrient concentrations. Finally, it is likely that the difference in GPP (and NPP) between these two lakes was greater than our data suggest, due to the possible underestimation of epipelon GPP in the open-water areas of Schulzensee. Periphyton biomass on plastic strips did not differ
significantly between our study lakes, but this was suspected to be an error due to the localized effect of floating-leaved plants in Schulzensee, which shaded the strips intended as open-water exposures. This was supported by data from the following year, when the monthly periphyton biomass accumulation on open-water strip exposures was higher in macrophyte-dominated Schulzensee (1.77 ± 0.2 μg chl a cm\(^{-2}\)) than in phytoplankton-dominated Gollinsee (1.08 ± 0.2 μg chl a cm\(^{-2}\); t-test, \(P = 0.05\)).

*Conceptual productivity model*

Our simple model predicts that a macrophyte-dominated, shallow lake supports higher rates of GPP than a more turbid, phytoplankton-dominated lake across an intermediate range of TP availability. A perturbation leading to the loss of submerged macrophytes and epiphyton at moderate nutrient concentrations may thus result in an immediate decrease in whole-lake GPP, assuming the disturbance does not significantly change the nutrient supply of the system. Within the parameters described for our lakes, the predicted difference between total GPP for alternative regimes disappears at mean lake depths greater than 4 m, or TP concentrations higher than 150 μg L\(^{-1}\). While this TP range may be applicable to other lakes with similar DOC concentrations to our study systems, much lower DOC concentrations would result in a larger modeled depth range across which macrophyte-dominated lakes would exhibit a higher GPP than phytoplankton-dominated lakes. Similarly, the TP threshold at which differences in GPP exist between regimes varies with mean depth, with shallower mean depths providing higher TP thresholds. As discussed above, differences in GPP between systems do not always match
differences in NPP (e.g. Blindow et al., 2006), and thus the details of our model results may differ slightly when NPP is considered.

A model by Genkai-Kato et al. (2012) describes a sudden increase in whole-lake GPP during a regime shift from periphyton to phytoplankton dominance, yet the types of lakes and the mechanisms involved for the regime shifts described in their study and our own are not analogous. Specifically, Genkai-Kato et al. (2012) focussed exclusively on lakes that do not feature submerged macrophytes, and the regulation of TP release by periphyton loss is a key mechanism by which their model predicts the relationship between regime shifts and whole-lake GPP. Our model does not account for an additional TP release from the sediments in a turbid regime, which is fitting as our results focus on a TP range below which periphyton production is expected to disappear completely as a result of phytoplankton shading (Liboriussen & Jeppesen, 2006). We further note that our modeled submerged macrophyte species (C. submersum) is rootless, and that rooted species may influence ambient nutrient conditions differently by using nutrients mainly from the sediment. However, all submerged macrophytes would theoretically influence phytoplankton nutrient availability by boosting epiphyton GPP and additionally suppress phytoplankton GPP by other mechanisms, such as allelopathy (Hilt & Gross 2008) and providing refuge to phytoplankton-grazing zooplankton (Timms & Moss, 1984). Overall, our model reflects conditions that are common in many shallow lakes capable of undergoing regime shifts (Scheffer et al., 1993a), and we suggest that the general relationship it illustrates is widely relevant.

Implications for lakes globally
This study presents both empirical and theoretical evidence to suggest that the GPP of small, eutrophic, shallow lakes is increased by the presence of a submerged macrophyte-epiphyton complex. We further suggest that a shift in such lakes to a phytoplankton-dominated regime may result in a decline in whole-lake GPP. This has important implications for freshwater systems globally, as the majority of lakes are small and shallow (Downing et al., 2006). Rosenzweig (1973) suggested that a loss of species richness (specifically across trophic levels) may be hazardous to ecosystem stability. With respect to regime shifts, Sand-Jensen et al. (2000) reported a widespread reduction in species richness in lakes with high phytoplankton turbidity. In this study, we describe a lowered structural (i.e. submerged macrophyte surface area) and ecological (i.e. number of primary producer groups) diversity in a system lacking submerged macrophytes, leading to a diminished whole-lake GPP. Our empirical results and simple productivity model thus indicate that a decline in productivity associated with the loss of submerged macrophytes may be a widespread phenomenon for shallow, eutrophic systems.
Acknowledgments

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Table 1 General characteristics of sampled lakes from two to four week sampling periods, early April 2010 to early April 2011, with standard error of the mean

<table>
<thead>
<tr>
<th></th>
<th>Gollinsee</th>
<th>Schulzensee</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(phytoplankton-dominated)</td>
<td>(macrophyte-dominated)</td>
<td></td>
</tr>
<tr>
<td>Surface area (m²)</td>
<td>33,000</td>
<td>39,000</td>
<td>-----</td>
</tr>
<tr>
<td>Z_mean (m)</td>
<td>1.7</td>
<td>2.2</td>
<td>-----</td>
</tr>
<tr>
<td>% Littoral area</td>
<td>18</td>
<td>32</td>
<td>-----</td>
</tr>
<tr>
<td>Light attenuation (m⁻¹)</td>
<td>$1.2 \pm 0.1\ (n = 17)$</td>
<td>$0.7 \pm 0.1\ (n = 16)$</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>pH</td>
<td>$7.9 \pm 0.1\ (n = 20)$</td>
<td>$7.6 \pm 0.1\ (n = 20)$</td>
<td>0.003</td>
</tr>
<tr>
<td>Total phosphorus (µg L⁻¹) *</td>
<td>$42 \pm 3\ (n = 20)$</td>
<td>$34 \pm 3\ (n = 20)$</td>
<td>0.07</td>
</tr>
<tr>
<td>SRP (µg L⁻¹) *</td>
<td>$4.69 \pm 0.55\ (n = 13)$</td>
<td>$4.38 \pm 0.55\ (n = 13)$</td>
<td>0.70</td>
</tr>
<tr>
<td>Total nitrogen (mg L⁻¹) *</td>
<td>$1.2 \pm 0.14\ (n = 3)$</td>
<td>$0.9 \pm 0.06\ (n = 17)$</td>
<td>0.07</td>
</tr>
<tr>
<td>Dissolved organic carbon</td>
<td>$12.3 \pm 0.3\ (n = 16)$</td>
<td>$11.3 \pm 0.3\ (n = 18)$</td>
<td>0.02</td>
</tr>
</tbody>
</table>

* Epilimnetic, pelagic means.
**Table 2** Gross productivity of primary producers with standard error of the mean

<table>
<thead>
<tr>
<th></th>
<th>Gollinsee GPP (g C m(^{-2}) y(^{-1}))</th>
<th>Schulzensee GPP (g C m(^{-2}) y(^{-1}))</th>
<th>(P)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Phytoplankton*</td>
<td>141 ± 8 ((n = 365))</td>
<td>182 ± 8 ((n = 365))</td>
<td>0.0006</td>
</tr>
<tr>
<td>Epiphyton*</td>
<td>10 ± 2 ((n = 365))</td>
<td>33 ± 2 ((n = 365))</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>Epipelon*</td>
<td>243 ± 15 ((n = 365))</td>
<td>258 ± 15 ((n = 365))</td>
<td>0.50</td>
</tr>
<tr>
<td><em>C. submersum</em></td>
<td>-----</td>
<td>27 ± 8</td>
<td>-----</td>
</tr>
<tr>
<td><em>A. stagnina</em></td>
<td>-----</td>
<td>22 ± 1 ((n = 80))</td>
<td>-----</td>
</tr>
</tbody>
</table>

* Means calculated from daily estimates
Table 3 Conceptual productivity model parameters

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Definition</th>
<th>Phytoplankton</th>
<th>Periphyton</th>
<th>Submerged Macrophytes</th>
</tr>
</thead>
<tbody>
<tr>
<td>$P_{\text{max}}$ (g C g chl $a^{-1}$ d$^{-1}$)</td>
<td>Maximum production</td>
<td>25$^1$</td>
<td>35$^1$</td>
<td>-----</td>
</tr>
<tr>
<td>$\alpha$ (g C g chl $a$ mol$^{-1}$ m$^{-2}$)</td>
<td>Specific efficiency of production</td>
<td>3$^1$</td>
<td>5$^1$</td>
<td>-----</td>
</tr>
<tr>
<td>$a^*$ (m$^2$ g chl $a^{-1}$)</td>
<td>Specific absorption of chl $a$</td>
<td>18.3$^1$</td>
<td>-----</td>
<td>-----</td>
</tr>
<tr>
<td>$\varepsilon_0$ (m$^{-1}$)</td>
<td>Background attenuation</td>
<td>0.61$^1$</td>
<td>-----</td>
<td>-----</td>
</tr>
<tr>
<td>$I_0$ (mol m$^2$ d$^{-1}$)</td>
<td>Mean PAR at water surface</td>
<td>19$^1$</td>
<td>-----</td>
<td>-----</td>
</tr>
<tr>
<td>Chl $a_{\text{max}}$ (g chl $a$ m$^{-2}$)</td>
<td>Maximum biomass</td>
<td>-----</td>
<td>-----</td>
<td>2.1$^2$</td>
</tr>
<tr>
<td>$n$</td>
<td>Power coefficient</td>
<td>-----</td>
<td>-----</td>
<td>3$^3$</td>
</tr>
<tr>
<td>$k_p$ (mg P m$^3$)</td>
<td>Half-saturation TP for chl $a$</td>
<td>14$^4$</td>
<td>14$^4$</td>
<td>50$^5$</td>
</tr>
<tr>
<td>$k_I$ (mol m$^2$ d$^{-1}$)</td>
<td>Half-saturation I for chl $a$</td>
<td>-----</td>
<td>2$^2$</td>
<td>4.7$^2$</td>
</tr>
<tr>
<td>$q_0$ (g P g chl $a^{-1}$)</td>
<td>Minimum cell quota</td>
<td>0.28$^4$</td>
<td>0.28$^4$</td>
<td>-----</td>
</tr>
<tr>
<td>$q_{\text{max}}$ (g P g chl $a^{-1}$)</td>
<td>Maximum cell quota</td>
<td>1.4$^4$</td>
<td>1.4$^4$</td>
<td>-----</td>
</tr>
</tbody>
</table>

Data from $^1$ present study, $^2$ Köhler et al. (2010), $^3$ van Nes et al. (2003), $^4$ Behrendt & Opitz (1996), $^5$ Jeppesen et al. (1990)
Table 4 Monthly and total whole-lake GPP with standard error of the mean

<table>
<thead>
<tr>
<th>Month</th>
<th>Gollinsee GPP (g C m⁻² d⁻¹)</th>
<th>Schulzensee GPP (g C m⁻² d⁻¹)</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>April</td>
<td>1.30 ± 0.08</td>
<td>1.60 ± 0.08</td>
<td>0.01</td>
</tr>
<tr>
<td>May</td>
<td>1.74 ± 0.14</td>
<td>1.50 ± 0.14</td>
<td>0.25</td>
</tr>
<tr>
<td>June</td>
<td>1.81 ± 0.18</td>
<td>3.50 ± 0.18</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>July</td>
<td>1.68 ± 0.11</td>
<td>4.23 ± 0.11</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>August</td>
<td>1.89 ± 0.17</td>
<td>3.21 ± 0.17</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>September</td>
<td>2.37 ± 0.13</td>
<td>1.27 ± 0.13</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>October</td>
<td>1.42 ± 0.08</td>
<td>0.88 ± 0.08</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>November</td>
<td>0.27 ± 0.02</td>
<td>0.45 ± 0.02</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>December*</td>
<td>0.03 ± 0.09</td>
<td>0.38 ± 0.16</td>
<td>0.07</td>
</tr>
<tr>
<td>January*</td>
<td>-----</td>
<td>0.28 ± 0.06</td>
<td>-----</td>
</tr>
<tr>
<td>February*</td>
<td>0.30 ± 0.51</td>
<td>1.00 ± 0.36</td>
<td>0.30</td>
</tr>
<tr>
<td>March*</td>
<td>0.80 ± 0.07</td>
<td>0.78 ± 0.07</td>
<td>0.87</td>
</tr>
<tr>
<td>Total</td>
<td>1.12 ± 0.06</td>
<td>1.60 ± 0.06</td>
<td>&lt; 0.0001</td>
</tr>
</tbody>
</table>

Note: Total GPP is weighted to a 365 day year. All monthly means are calculated from estimates for each day of the month, except

* March estimates only available after ice-break (n = 16 for both lakes), December n are 15 for Gollinsee and 5 for Schulzensee, January n are 2 for Schulzensee, February n are 3 for Gollinsee and 6 for Schulzensee, with one high outlier excluded from Schulzensee as it occurred during ice-break when O₂ fluxes may have been poorly quantified.
Figure Legends

Figure 1 Seasonal comparison of a) periphyton and b) phytoplankton GPP between lakes (g C m\(^{-2}\) d\(^{-1}\)). Boxes represent the upper quartile, median, and lower quartile, and whiskers represent the 5\(^{th}\) and 95\(^{th}\) percentiles. Central squares represent the mean, and crosses designate minimum and maximum values. Goll. represents Gollinsee, and Schulz. represents Schulzensee.

Figure 2 Monthly calculated GPP (mg C m\(^{-2}\) d\(^{-1}\)) in a) phytoplankton-dominated Gollinsee and b) macrophyte-dominated Schulzensee. Boxplots present O\(_2\) curve-derived GPP, with boxes representing the upper quartile, median, and lower quartile, and whiskers representing the 5\(^{th}\) and 95\(^{th}\) percentiles. Central squares represent the mean, and crosses designate minimum and maximum values. Columns present compartmental GPP calculations. One high outlier (7160 mg C m\(^{-2}\) d\(^{-1}\)) is excluded from Schulzensee in February as it occurred during ice-break when fluxes may have been poorly quantified.

Figure 3 Conceptual model displaying the theoretical response of individual primary producer group (left boxes) and whole-lake (right boxes) GPP (g C m\(^{-2}\) d\(^{-1}\)) to TP availability with (“M”) and without (“P”) submerged macrophytes. Model outputs are provided for lakes of mean depth 1.5 m (top), 2.5 m (middle) and 3.5 m (bottom).
Fig. 1

(a) Periphyton GPP (g C m$^{-2}$ d$^{-1}$) for Spring, Summer, and Autumn.

(b) Phytoplankton GPP (g C m$^{-2}$ d$^{-1}$) for Goll. Schulz. in Spring, Summer, and Autumn.
Fig. 2

(a) Gollinsee

- Other (C. submersum and A. stagnina)
- Epiphyton
- Epipelon
- Phytoplankton

Gross primary production (mg C m$^{-2}$ d$^{-1}$)

(b) Schanzensee

Month: Apr May Jun Jul Aug Sep Oct Nov Dec Jan Feb Mar Apr
Fig. 3

![Graph showing gross primary production vs. phosphorus concentration](image)