

Drivers of metabolism and net heterotrophy in contrasting lakes

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Abstract

We investigated the influence of light, nutrients, and organic matter on gross primary production (GPP), ecosystem respiration (R), and net ecosystem production ($NEP = GPP - R$) in a dystrophic forest lake and an open eutrophic lake. Forest vegetation reduced incoming irradiance (20%) and wind speed (34%) in dystrophic Grib sø, having thermal stratification 1 month longer than in eutrophic Slot sø. While Grib sø had nutrient-limited phytoplankton during most of the year, Slot sø only experienced nutrient depletion during algal blooms. Colored dissolved organic matter (CDOM) absorbed most light (average 82%) in dystrophic Grib sø, while phytoplankton and other particles absorbed most light (45%) in eutrophic Slot sø. GPP and NEP were positively related to irradiance in both lakes. However, because of higher CDOM absorbance, three times more light was needed to attain autotrophy in Grib sø, being net heterotrophic ($NEP < 0$) for 79% of all days, compared to 59% in Slot sø. This difference vanished when NEP was scaled to light absorption by pigments, although the eutrophic lake maintained a higher photon yield. Metabolic rates varied much more in Slot sø, where higher light and nutrient availability facilitated occasional phytoplankton blooms, while low light and nutrient availability in Grib sø dampened temporal variability. Both lakes were annually net heterotrophic with similar annual areal rates ($NEP, -14 \text{ mol C m}^{-2}$). Net heterotrophy in dystrophic Grib sø derives from high import of organic carbon-rich water, while heterotrophy in eutrophic Slot sø is fueled by degradation of sediment pools of organic matter accumulated under previous hypereutrophic conditions, emphasizing the importance of lake history on the contemporary metabolic state.

Lakes in forest catchments receive less light and easily accessible dissolved nutrients for phytoplankton production than lakes in agricultural landscapes (Jackson and Hecky 1980; Sand-Jensen and Staehr 2007). Input of organic detritus from the forest stimulates growth and metabolism of bacteria and zooplankton, enhances community respiration (R), and constrains phytoplankton gross primary production (GPP) due to shading from colored dissolved organic matter (CDOM, Christensen et al. 1996; Jonsson et al. 2003). Rates of net ecosystem production ($NEP = GPP - R$) can be used to evaluate the trophic state of a lake ecosystem. Consequently, brown-colored forest lakes should display stronger net heterotrophy ($NEP < 0$) than open, clear-water lakes (del Giorgio et al. 1999; Sobek et al. 2005). While increasing nutrient richness is believed to stimulate autotrophy more than heterotrophy (Cole et al. 2000), input of easily degradable organic matter and degradation of accumulated sediment material will have the opposite effect (Schindler et al. 1997). It is, therefore, possible that eutrophic lakes can still exhibit distinct net heterotrophy, one aspect we will examine in this study.

Net autotrophic systems ($NEP > 0$) produce significantly more organic material than they degrade. The excess organic material may either be exported to adjacent systems and/or accumulate within the system in the sediment or as dissolved organic matter in the water. Export from and accumulation of organic material within the system may, nevertheless, also occur in net heterotrophic systems ($NEP < 0$). But compared to net autotrophic

systems, the higher R than GPP in net heterotrophic systems typically relies on a net import of organic material from outside. Net heterotrophy could also result from net degradation of accumulated organic pools during periods of low production caused by reduced nutrient loading. Thus, while all systems import and export, as well as accumulate, produce, and degrade organic material, the balance between these processes, identified by the balance between GPP and R , determines whether systems are net autotrophic or net heterotrophic. On a global scale, GPP: R and NEP help in understanding global carbon cycling and explicitly defining the role of ecosystems as sources or sinks of atmospheric CO_2 (del Giorgio and Duarte 2002; Karl et al. 2003).

Metabolism is driven by different forces at different timescales. Significant diel oscillations in GPP and NEP develop in ecosystems as a response to the diurnal light cycle. Since most photosynthetic organisms in lake ecosystems live longer than a day, variations in irradiance between days and weeks will affect ecosystem metabolism on these temporal scales. Variations in metabolism over months, seasons, and years, however, reflect changes in ecosystem structure and activity of different trophic groups (Smith and Hollibaugh 1997). Such long-term changes can occur as a response to ecosystem succession, eutrophication, invasion of new species, and climate change. Nutrient enrichment, for example, can push lakes from net heterotrophy to net autotrophy by stimulating GPP more than R (Schindler et al. 1997; del Giorgio et al. 1999). Greater inputs of dissolved organic matter stimulate R (del Giorgio and Duarte 2002) and may even reduce GPP

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Table 1. Basic lake variables for Gribssø and Slotssø. Data from Rasmussen (1999).

Variables	Gribssø	Slotssø
Area (km ²)	0.10	0.22
Fetch (m)	276	403
Max depth (m)	11	9
Mean depth (m)	4.8	3.5
Volume (10 ⁶ m ³)	0.484	0.705
Forest cover (%)	90	17
Water residence time (yr)	2.1	0.5

because of greater light attenuation in the water (Karlsson et al. 2009) and, thereby, lead to net heterotrophy (del Giorgio and Peters 1994; Carpenter and Pace 1997; Krause-Jensen and Sand-Jensen 1998).

While it is well known that addition of inorganic nutrients may shift the annual balance between gross primary production and respiration in lakes (Cole et al. 2000), knowledge concerning the influence of the surrounding forest on lake metabolism through shading, lower wind exposure, and higher input of organic matter is limited (Sand-Jensen and Staehr 2007). Especially small forest lakes receive less light than larger and more open lakes. Forest lakes furthermore receive slowly decomposable organic material from the terrestrial vegetation, which contributes to a larger attenuation of the sparser surface irradiance, further reducing the GPP : *R* ratio (Sand-Jensen and Staehr 2007).

This study investigates and compares the importance of physical, chemical, and biological drivers of day-to-day and seasonal variability in lake metabolism in a dystrophic forest lake and a nutrient-rich open lake. The first specific goal was to quantify the proportions of light attenuation attributable to CDOM, phytoplankton, other particles, and water and test the hypothesis that primary production can be primarily limited by light in a nutrient-poor dystrophic lake (Karlsson et al. 2009). The second specific goal was to determine the seasonal patterns of ecosystem metabolism (GPP, *R*, and NEP) and test their correlation to temperature, available light, and inorganic nutrients in the mixed surface waters or to biomass and light absorption of phytoplankton. We examined how close GPP and *R* are temporally coupled and whether NEP follows a characteristic seasonal trend. The third specific goal was to test whether greater nutrient richness in the eutrophic lake enhances the temporal variability of phytoplankton biomass and production, while high and

constant concentration of dissolved organic matter in the forest lake restricts their temporal variability. Finally, we established an annual carbon budget for each lake to further evaluate the implications of different types of carbon inputs for lake metabolism.

Methods

Study sites—The study was conducted from April to November 2006 in two Danish lakes, Gribssø (55°59'N, 12°18'W) and Frederiksborg Slotssø, hereafter Slotssø (55°56'N, 12°17'W) located 9 km from each other. Both lakes are small, shallow, and stratified most of the summer (Table 1). The littoral zone is small with virtually no submerged plants, since less than 10% of the bottom areas are shallower than 1 m and Secchi transparency is typically less than 1 m. Gribssø is a dystrophic, dark-stained low-productivity lake primarily fed by surface streams. Slotssø is also fed by surface streams but is highly productive and has reoccurring algal blooms (Staehr and Sand-Jensen 2007).

Monitoring station—Oxygen concentration, wind speed, temperature, and irradiance in air and at different depths in the water were measured continuously and averaged every 10 min using sensors mounted on a floating raft in the center of the lakes (Table 2 shows location of sensors and manufacturers). Oxygen and irradiance sensors were cleaned every second week, and oxygen calibration was checked and reset. Electrode drift was small and was corrected with the assumption that it is linear over time.

Profiles and water analyses—Depth profiles of oxygen and temperature were recorded by a Yellow Springs Instrument (YSI) 600XL multisonde at every visit to the monitoring stations. Water was collected from the epilimnion for measurements of chlorophyll *a* (Chl *a*), dissolved organic matter, and inorganic nutrients. Samples for Chl *a* and pheopigments were filtered through Advantec® GC-50 filters, extracted in 96% ethanol for 24 h, and measured spectrophotometrically according to Parsons et al. (1984). Absorbance of colored dissolved organic matter (CDOM) was measured in a GF/F filtrate (0.7 μm) at 300, 340, 360, 400, and 440 nm through a 5-cm cuvette. In comprehensive measurements from Danish lakes and streams, DOC concentrations (mg C L⁻¹) increased linearly with CDOM absorbance at 360 nm (m⁻¹): DOC = 0.454 CDOM₃₆₀ + 1.9 (*r*² = 0.80, *n* = 399, C. Stedmon unpubl. data)

Table 2. Parameters recorded by the monitoring stations from April to December 2006 in Gribssø and Slotssø and specifications regarding instruments, frequency, and locations of measurements.

Parameter	Sensor	Frequency (min)	Depth (m)
%O ₂	Oxyguard	10	-0.5
Wind speed	Hobo	10	+ 1.0
Water temperature	Stow away tidbit	10	-0.5, -1, -2, -3, -4, -5, -6, -7, (-10 only Gribssø)
Irradiance	In air: Hobo 2π quantum sensor	10	+ 1.0
	In water: Odyssey 2π quantum sensor	10	-0.1, -0.4, -1.0

permitting estimation of DOC from CDOM. Nitrate was quantified using a rapid flow analyzer Alpkem (Alpkem 1990); ammonia was determined according to Solorzano (1969); and phosphate and silica were determined according to Strickland and Parsons (1968).

Oxygen flux—Oxygen concentrations recorded every 10 min were used to calculate net ecosystem production (NEP) for 30-min intervals, according to $NEP_{30min} = \Delta O_2 - D/Z_{mix}$ (Cole et al. 2000), where ΔO_2 (mmol O₂ m⁻³ 30 min⁻¹) is change in oxygen concentration over 30 min, D (mmol O₂ m⁻² 30 min⁻¹) is exchange with the atmosphere in this period, and Z_{mix} (m) is mixing depth. Atmospheric exchange was calculated as $D = k(O_2 - O_{2sat})$, where O_2 is actual oxygen concentration, O_{2sat} is oxygen concentration in water in equilibrium with the atmosphere at ambient temperature, and k is oxygen exchange calculated for each time step from the estimate of k_{600} and the ratio of Schmidt numbers as $k = k_{600} ((Sc/600)^{-0.5})$ according to Jahne et al. (1987). k_{600} (k for a Schmidt number (Sc) of 600) was estimated as a function of wind speed at 10 m above the lake surface as k_{600} (cm h⁻¹) = $2.07 + 0.215 U^{1.7}$ according to Cole and Caraco (1998). Assuming a neutrally stable boundary layer, wind speed (U) at 10 m was calculated from our measurements at 1 m using the relationship in Smith (1985). Because there is no photosynthesis at night, we assume nighttime R equals nighttime NEP measured from 1 h past sunset until 1 h before sunrise. Assuming that the daytime rate of R is equal to the nighttime rate (Hanson et al. 2003; Lauster et al. 2006), we calculated daily respiration rates as hourly R during nighttime $\times 24$ h. GPP was determined as the sum of daytime NEP and R , and daily NEP was finally calculated as $GPP - R$ (where R is in positive numbers). It is likely that daytime R exceeds nighttime R (Tobias et al. 2007), which would underestimate GPP and R , but would have no effect on NEP (Cole et al. 2000). For ease of comparison, we present GPP values as positive and R values as negative. Volumetric metabolic rates (mol O₂ m⁻³ d⁻¹) were turned into areal rates by multiplying with the lake volume of the upper mixed layer and dividing by the lake surface area, where the lake volume of the upper mixed layer was calculated by combining mixing depth with a hypsographic table.

Light attenuation and light availability—The vertical light attenuation coefficient (K_D , 400–700 nm) was determined as the slope of a linear regression model of irradiance (E_z) vs. depth (z): $\ln(E_z) = b + K_D z$. Continuous irradiance recordings integrated over 30-min intervals allowed 10–24 values of K_D to be determined each day. Only regression models with $r^2 > 0.8$ were accepted when computing daily average K_D values. Fouling of the underwater light sensors occurred during summer, especially in the eutrophic Slotssø. Comparing values before and after cleaning, however, only caused minor increases of calculated K_D values because sensors at different depths became almost equally fouled with time.

Daily light availability (E_{mean} ; mol photons m⁻² d⁻¹) was calculated as an average for the mixed surface zone.

With data for daily surface irradiance (E_0 ; mol photons m⁻² d⁻¹), mixing depth (Z_{mix} ; m), and light attenuation (K_D ; m⁻¹), with a constant of 0.1 for backscattering and surface reflection, β (Kirk 1994), E_{mean} was calculated from Eq. 1, modified from Riley (1957):

$$E_{mean} = E_0(1 - \beta)(1 - e^{-K_D Z_{mix}})/(K_D Z_{mix}) \quad (1)$$

A photon budget was constructed according to Sand-Jensen and Staehr (2007) at each sampling by calculating relative absorption at each wavelength as the fraction of surface light absorbed by each of the four main attenuation components, water, CDOM, pigments, and nonpigmented particles–detritus relative to the total absorption budget.

Physical mixing—High-frequency water temperature data were used to determine mixing depth (Z_{mix}) as the depth with the maximum temperature gradient by applying an empirical curve-fitting equation to temperature profiles every 10 min according to a model described in Closter (2007). Logged temperature profiles were also used to calculate the stability of thermal stratification at the predicted mixing depth using the Brunt–Väisälä buoyancy frequency N (s⁻¹), (Gill 1982).

Carbon balance—The annual carbon budget was established to evaluate the importance of carbon import, export, and storage for the differences and magnitudes of measured annual net ecosystem production (NEP). According to Cole et al. (2007), daily values of NEP are in theory equivalent to a carbon mass balance computed from import–export budgets (Kemp et al. 1997), since NEP is equal to carbon export (C_{export}) and storage ($\Delta C_{storage}$) minus carbon import (C_{import}): $NEP = \Delta C_{storage} + C_{export} - C_{import}$. Net heterotrophy ($NEP < 0$) occurs when carbon import exceeds export and no storage takes place, or when export and import are equal and organic pools accumulated within the system's boundaries are degraded. Annual NEP measured as oxygen was converted to carbon units using a molar ratio of 1.25 (Grande et al. 1989). Import of carbon was estimated by multiplying annual water inflow Q (m³ yr⁻¹) from streams, groundwater, and net precipitation with measured concentrations of total organic carbon (TOC) (mol C m⁻³) and adding litter fall assuming an annual carbon input of 500 g C per meter of the lake periphery covered by trees (Fisher and Likens 1973). Carbon export was estimated by multiplying annual water outflow via streams and groundwater with lake carbon concentrations. Storage was calculated as $\Delta C_{storage} = NEP - C_{export} + C_{import}$.

Annual water balance was established by a combination of measurements and modeling. Local meteorological data on precipitation, air temperature, relative humidity, and wind speed was used in combination with surface water temperatures to determine evaporation according to a mass-transfer approach (Dingman 2008). For Slotssø, we estimated stream input and output as well as groundwater exchange, from empirical relationships with precipitation, given in a study by Rasmussen (1999). For Gribssø, groundwater exchange was determined through measure-

ments of hydraulic heads in 16 piezometers placed at the periphery of the lake for 3 months (Rosenberry et al. 2008). Since groundwater input was very low (850 L d^{-1}) and constant, periods with increasing water level could be used to calculate stream inflow as the residual between increases in lake volume and the sum of net precipitation and loss via groundwater output. Changes in lake volume in Gribsø were determined by combining daily water level recordings during 2006 with a hypsograph. Estimated stream flow compared well with four measurements made during winter and spring.

For Slotssø, total phosphorus (TP) concentration in stream input was measured on four occasions and found to be at the same level as in 1999. Monthly measurements of TP in 1999 showed that TP in the stream outlet corresponded to lake surface values ($r^2 = 0.70$, $p < 0.01$), allowing TP output concentrations to be calculated from lake measurements in 2006. TOC concentrations (mg L^{-1}) were finally calculated from TP (mg L^{-1}) using a TOC to TP ratio of 160 established from previous measurements on 25 Danish lakes (P. Stæhr unpubl. data). Deposition of TOC via rain was measured 20 km west of the lakes on seven occasions in 2006. Concentrations averaged $9.5 \pm 2 \text{ mg C L}^{-1}$ ($\pm \text{SE}$). At Gribsø, TOC was measured according to the procedure in Kragh and Sondergaard (2004). TOC in the stream inlets averaged ($100 \pm 10 \text{ mg C L}^{-1}$) with less in groundwater entering ($50 \pm 5 \text{ mg C L}^{-1}$) and little TOC leaving ($10 \pm 1 \text{ mg C L}^{-1}$) the lake. Similar groundwater concentration values were used in the Slotssø carbon budget.

Statistical analysis—Simple correlations between metabolic rates and physical and chemical drivers were evaluated using the Pearson correlation analysis. Empirical models of the variation in GPP, R , and NEP were analyzed by regression analysis. However, as with most other time series data, the ordinary regression residuals were highly autocorrelated over time (evaluated using the Durban–Watson autocorrelation coefficient). In order to account for autocorrelation, multiple regression models were expanded by regression with autocorrelated errors (Proc Autoreg, SAS Institute 1994), thereby accounting for the autocorrelation of the errors. All data analysis was done using SAS STAT (SAS Institute 1994).

Results

Physical and chemical changes—Stratification began 4 d earlier and lasted 26 d longer in the wind-protected forest lake, Gribsø, than in Slotssø (Fig. 1). Despite a greater mean depth, the thermocline was located higher up in the water column in Gribsø ($3.8 \pm 1.1 \text{ m}$; mean \pm standard deviation [SD]) than in Slotssø ($4.9 \pm 1.0 \text{ m}$). Relationships between temperature, stability, and stratification depth were stronger in Gribsø than Slotssø (Table 3).

Mean daily surface irradiance was 20% lower in Gribsø than Slotssø because of shading from the forest surrounding Gribsø. Mean annual light availability in the mixed surface waters (Fig. 1), calculated from daily data on surface irradiance, light attenuation, and mixing depth, was

also 20% lower in Gribsø, despite the 1 m lower mixing depth. Wind speeds were low but slightly higher and more variable in Slotssø ($2.8 \pm 1.2 \text{ m s}^{-1}$) than the more wind-protected Gribsø ($2.1 \pm 0.9 \text{ m s}^{-1}$). Although wind speeds during summer were lower than 4 m s^{-1} during 92% of the time in Slotssø and 97% in Gribsø, occasional high wind speeds significantly deepened the mixed layer, particularly in Slotssø (Table 3).

Dissolved oxygen in the epilimnion in Gribsø was undersaturated at noon in 82% of all days and exhibited little variability ($88 \pm 13\% \text{ O}_2$; mean \pm SD), while Slotssø was supersaturated in 56% of all days and varied more ($107 \pm 40\% \text{ O}_2$). Thermal stratification caused an immediate oxygen decline in the hypolimnion, though much faster in Slotssø than Gribsø (Fig. 1). Deeper water and a shallower thermocline in Gribsø resulted in anoxia in 30% of the lake volume and 55% of the sediment area in late summer, compared to 11% of the volume and 27% of the sediment area in Slotssø.

Inorganic nutrients in the epilimnion were depleted shortly after the onset of stratification (Fig. 2). With half-saturation constants for uptake of N ($\sim 2.5 \mu\text{mol L}^{-1}$; Eppley et al. 1969), P ($\sim 0.2 \mu\text{mol L}^{-1}$; Furnas et al. 1976), and Si ($\sim 2.5 \mu\text{mol L}^{-1}$; Azam and Chisholm 1976), potential nutrient limitation of phytoplankton growth occurred during 60% of the time in Gribsø and 20% in Slotssø (Fig. 2). Nutrient limitation resulted from low levels of nitrogen (nitrate + ammonia) in Gribsø, while phosphorus was the main limiting nutrient in Slotssø. Sudden summer peaks of epilimnion phosphorus in both lakes (Fig. 2) suggested P injection from bottom waters during deeper mixing.

Organic matter and light attenuation—Light absorption by CDOM was threefold higher in Gribsø than Slotssø. Gradual decrease of CDOM in Gribsø from spring to late summer results from a combination of microbial consumption, bleaching of humic substances at high irradiances, and low inputs of DOC. High CDOM absorption is reestablished during autumn and winter by large surface runoff from the forest (Fig. 2). The sudden rise of CDOM in autumn coincides with termination of stratification and redistribution of CDOM accumulated in the hypolimnion during summer. In eutrophic Slotssø, a significant increase in CDOM was observed during summer ($r = 0.57$, $p < 0.01$), during a period of decreasing DOC input via streams, suggesting that CDOM in Slotssø mostly derives from the high phytoplankton production. This notion is supported by the positive correlation between Chl a and CDOM ($r = 0.56$, $p < 0.01$) when allowing for a 1-month time lag for CDOM to be released from degrading phytoplankton.

Chlorophyll a concentrations were highly variable in Slotssø (3 to $216 \mu\text{g L}^{-1}$) with blooms of diatoms occurring during spring and blooms of green algae and cyanobacteria during summer (K. Christoffersen pers. comm.). Each bloom was followed by a clear-water phase, suggesting that seasonal variability in algal abundance was determined by a combination of nutrient and light availability influencing phytoplankton growth and zooplankton grazing influencing losses (Fig. 2). Diatom blooms depleted silica and late

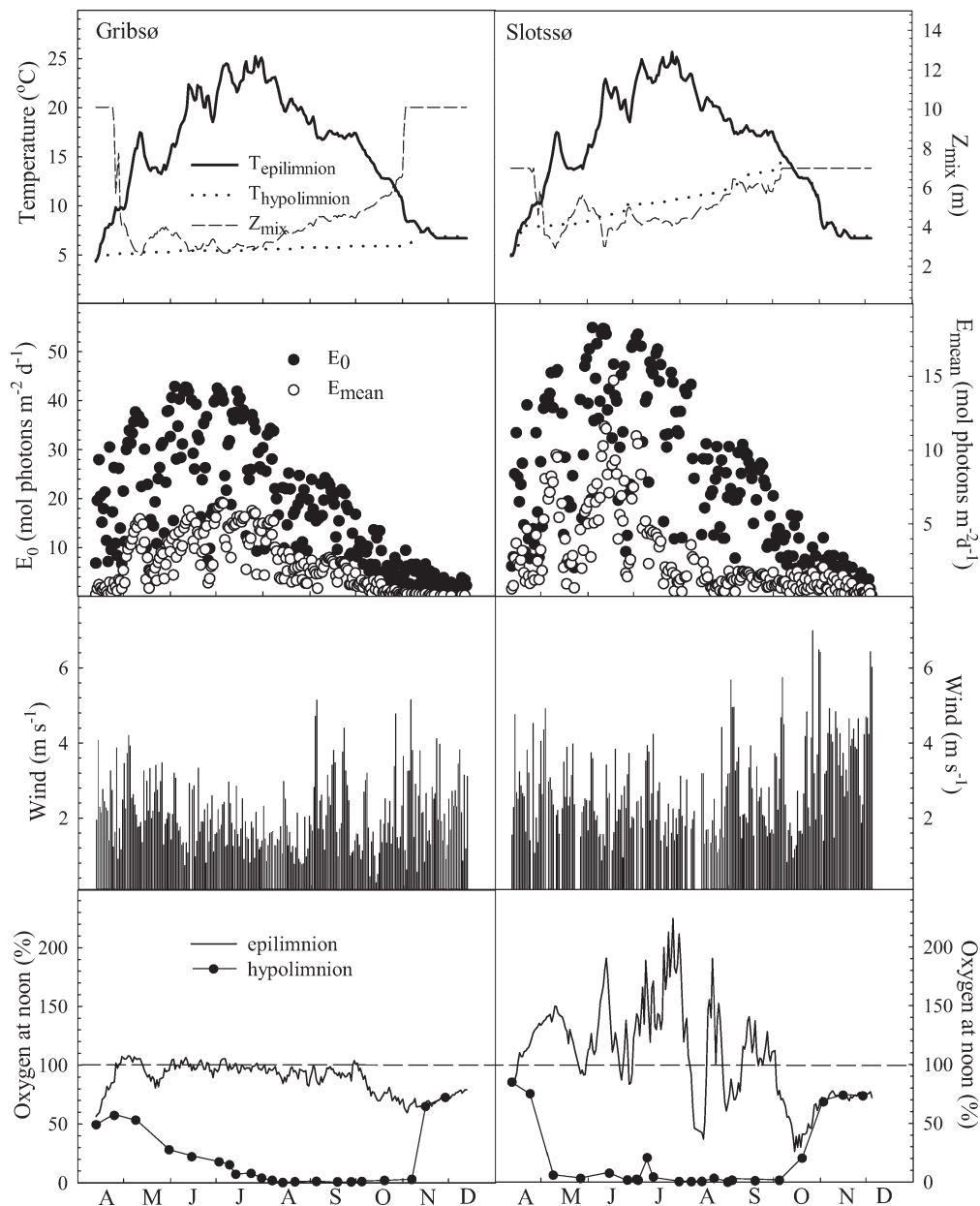


Fig. 1. Seasonal changes in daily water temperature, calculated mixing depth (Z_{mix}), surface irradiance (E_0), mean irradiance (E_{mean}) in mixed surface layer, wind speed calculated at 10 m above the lake surface, and measurements of oxygen saturation in surface (daily) and bottom (biweekly) water.

summer blooms of cyanobacteria depleted orthophosphate (Fig. 2). Algal densities were much lower (5 to $61 \mu\text{g L}^{-1}$) with no distinct blooms in Gribssø and potential nutrient limitation most of the summer (Fig. 2). Algal blooms and collapses in Slotssø were mirrored by highly variable surface concentrations of oxygen, while concentrations were almost constant in Gribssø (Fig. 2).

The light attenuation coefficient, K_D , showed a high, stable, and slowly decreasing level in Gribssø closely related ($r^2 = 0.94$) to changes in absorbance of CDOM. In comparison, K_D was much lower in Slotssø, though with several distinct peaks related ($r^2 = 0.98$) to changes in algal

biomass (Fig. 2). Consequently, the lower mean light availability for primary production in the upper mixed surface layer in Gribssø was closely regulated by high absorption by CDOM, while in Slotssø self-shading of phytoplankton was the main determinant of light availability. This pattern is confirmed by photon budgets determining the percentages of light attenuation attributable to CDOM, Chl *a*, other particles, and water alone (Fig. 3). In Gribssø, CDOM attenuated the majority of light throughout the year (average 82%; Fig. 3). In Slotssø, Chl *a* accounted for 50–60% of light absorption during phytoplankton blooms. The annual mean absorption by

Table 3. Pearson correlation coefficients for Gribssø and Slotssø between daily estimates of gross (GPP) and net (NEP) ecosystem production, respiration (R), autotrophy : heterotrophy (GPP : R) and environmental variables. Epilimnion temperature (T_{epi}), daily mean irradiance (E_0), mean wind speed at 10 m above surface, mixing depth (Z_{mix}), Brunt–Väisälä buoyancy frequency (N), Chl a , and DOC.

Lake	Parameter	NEP	R	GPP : R	T_{epi}	E_0	Wind	Z_{mix}	N	Chl a	DOC
Gribssø ($n = 244$)	GPP	0.17**	0.92***	0.55***	0.58***	0.55***	-0.29***	-0.60***	0.59***	0.26***	-0.05
	NEP		-0.24***	0.75***	0.32***	0.55***	-0.02***	-0.35***	0.31***	0.12*	0.08
	R			-0.24***	0.44***	0.32***	-0.27***	-0.47***	0.46***	0.20**	-0.08
	GPP : R				0.61***	0.72***	-0.19**	-0.67***	0.62***	0.38***	-0.06
	T_{epi}					0.63***	-0.27***	-0.88***	0.99***	0.60***	-0.44***
	E_0						-0.05	-0.66***	0.54***	0.25***	-0.10
	Wind							0.18**	-0.27***	-0.17**	0.13*
	Z_{mix}								-0.90***	-0.59***	0.28***
	N									0.55***	-0.52***
	Chl a										-0.57
	Slotssø ($n = 215$)	GPP	0.21**	0.91***	0.30***	0.73***	0.51***	-0.46***	-0.49***	0.72***	0.72***
NEP			-0.21**	0.73***	0.22**	0.46***	-0.18**	-0.36***	0.35***	0.11	-0.34***
R				-0.01	0.63***	0.32***	-0.37***	-0.34***	0.58***	0.66***	0.07
GPP : R					0.32***	0.65***	-0.31***	-0.55***	0.50***	0.22**	-0.44***
T_{epi}						0.65***	-0.32***	-0.72***	0.93***	0.63***	-0.33***
E_0							-0.30***	-0.75***	0.72***	0.26***	-0.42***
Wind								0.31***	-0.36***	-0.29***	0.18**
Z_{mix}									-0.85***	-0.36***	0.44***
N										0.63***	-0.36***
Chl a											-0.12

* $p < 0.05$.

** $p < 0.01$.

*** $p < 0.001$.

phytoplankton and other particles was 45% in Slotssø, where absorption by CDOM, likely deriving from phytoplankton production, was still appreciable (average 37%).

Temporal pattern in ecosystem metabolism—Rates of GPP and R increased during spring, reached a maximum in summer, and declined in autumn and winter in both lakes (Fig. 4A,B). Temporal variability in GPP and R was most pronounced in Slotssø, showing several distinct peaks along with phytoplankton blooms. Seasonal trends in NEP were less distinct, but values remained negative from mid-September to December during deepening and final loss of the thermocline and mixing of anoxic bottom waters into the water column. Likewise, the seasonal trend of the GPP : R ratio was the same in both lakes, with net autotrophy (GPP : $R > 1.0$) occurring during certain spring and summer periods and net heterotrophy prevailing in autumn–winter (Fig. 4C). Gribssø was net heterotrophic (NEP < 0) in 79% of all days, while Slotssø was net heterotrophic in 57% of all days and net autotrophic (NEP > 0) in spring and summer during establishment of phytoplankton blooms (Fig. 4A,B). On an areal basis NEP amounted to $-18 \text{ mol O}_2 \text{ m}^{-2} \text{ yr}^{-1}$ in Gribssø and $-17 \text{ mol O}_2 \text{ m}^{-2} \text{ yr}^{-1}$ in Slotssø.

Day-to-day variations in metabolic rates expressed by the coefficient of variation ($\text{CV} = \text{SD}/\bar{X} \times 100\%$) were much larger in Slotssø (95% for GPP, 91% for R , and 11% for NEP) than Gribssø (66%, 56%, and 1%), reflecting the stronger and more stochastic behavior of phytoplankton and associated heterotrophs in Slotssø in contrast to their more dampened behavior in CDOM-rich and more nutrient-poor Gribssø.

Regulation of ecosystem metabolism—Rates of GPP and R were positively correlated with temperature and surface irradiance (Fig. 5; Table 3) reflecting the contrasts between high summer rates from mid-May to mid-September and low rates outside this period. Metabolic rates were negatively related to increasing mixing depth due to both the seasonal contrasts between deep mixing in winter and shallower mixing in summer at higher temperature and the constraints on GPP and consequently on NEP caused by lower available irradiance to phytoplankton during deeper vertical mixing. The level of autotrophy (GPP : R and NEP) also responded positively to irradiance and temperature but negatively to increasing mixing depth (Table 3).

The relative importance of physical and biological drivers for GPP, R , and NEP was evaluated by multiple regression analysis. Temperature and DOC were the best predictors of daily GPP and R in Gribssø, whereas algal biomass and temperature were the best predictors in Slotssø (Table 4). In both lakes, GPP and R increased with water temperature, whereas NEP decreased and GPP and NEP increased with irradiance and decreased with mixing depth. In Gribssø, R increased more than GPP with DOC, causing NEP to decrease. DOC was also negatively related to NEP in Slotssø (Table 3) but not significantly (Table 4).

Three times more light was required as an average for the mixed layer to attain autotrophy in Gribssø ($4.8 \text{ mol m}^{-2} \text{ d}^{-1}$) than in Slotssø ($1.7 \text{ mol m}^{-2} \text{ d}^{-1}$), probably because three times less light is absorbed by photosynthetic pigments in Gribssø than Slotssø (Fig. 6). Thus, when NEP was expressed as a function of the daily incident irradiance absorbed by photosynthetic pigments, the two lakes

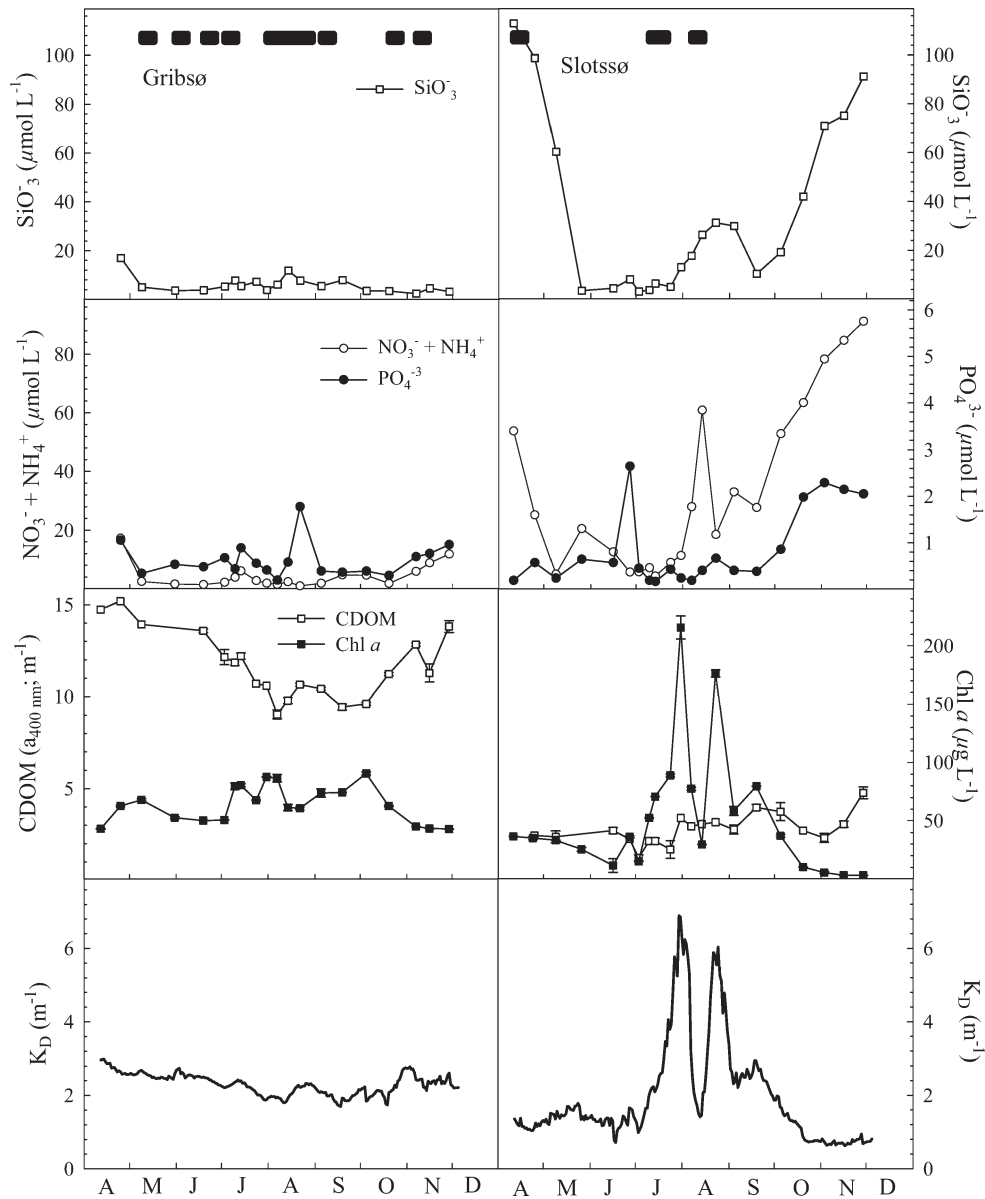


Fig. 2. Seasonal changes in concentrations of inorganic nutrients, dissolved organic material, Chl *a*, and light attenuation coefficients. Periods of potential nutrient limitation for algal growth (horizontal bars in uppermost panel) were designated when concentrations of N, P, or Si fell below their respective half-saturation constants (*see text*).

resembled each other by requiring about the same absorbed photon flux (5–6 mol m⁻² d⁻¹) to reach NEP = 0, though with a higher slope ($p < 0.05$, Student *t*-test) for Slotssø (0.065 mol O₂ mol⁻¹ photon) than Gribssø (0.046), reflecting higher photosynthetic efficiency in the use of absorbed photons (Fig. 7).

Organic carbon budget—Gribssø receives almost all its carbon through streams (92%), with only minor inputs from groundwater (1%), litter fall (3%), and rainwater (4%; Fig. 8). Most of this material is mineralized within the lake (89%), with only small storage (1%) and some export via groundwater (10%). In comparison, Slotssø imports about

two times less organic carbon per m² and exports slightly more than it imports (Fig. 8). Since Slotssø is annually net heterotrophic (NEP: -13.6 mol C m⁻² yr⁻¹), evasion of carbon to the atmosphere probably derives from mineralization of lake sediments.

Discussion

Importance of physical and chemical conditions—Dystrophic Gribssø received less light, was more wind protected, and had three times higher light absorption by dissolved organic matter than the open Slotssø. Both lakes showed signs of nutrient-limited phytoplankton growth, but

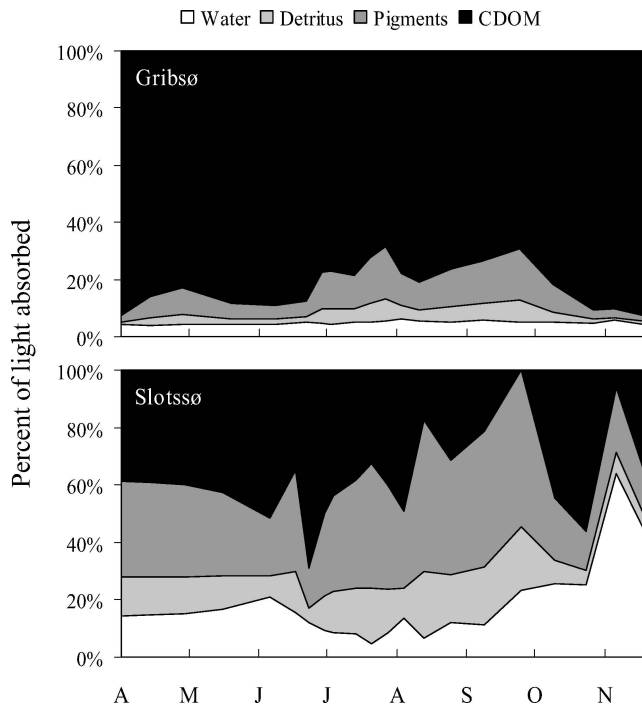


Fig. 3. Seasonal changes in the relative contribution of different light absorbing components to total light attenuation.

nutrient depletion was more pronounced and algal biomass significantly lower in Gribssø than Slotssø. External inputs of dissolved inorganic nutrients are relatively low in both lakes, and the higher P levels in Slotssø (Fig. 2) probably derive from internal release from historically enriched sediments, causing profound phosphate accumulation in anoxic bottom waters during summer (Andersen et al. 1979). The weaker and more variable thermal stratification (Fig. 1) permits occasional mixing of the water column in Slotssø during summer and injects nutrient-rich bottom waters into surface waters and stimulates phytoplankton biomass and productivity, making the lake net autotrophic during summer.

Differences in the duration and strength of thermal stratification are primarily related to wind exposure, fetch, and lake depth (Gorham and Boyce 1989; Demers and Kalff 1993). Gribssø is significantly more sheltered (34% lower wind speed) by the surrounding forest and has a lower fetch and a greater depth than Slotssø, which can account for differences in the strength of stratification (see Table 2). Thus, for the same average wind speed of 2 m s^{-1} across the lake surface, Gribssø needed 43 d to become fully mixed in June–August compared to only 17 d in Slotssø according to a hydrodynamic model (Closter 2007). The location of the thermocline is largely dependent on wind-induced mixing, which increases with the fetch (Closter 2007), but stratification depth is shallower in small lakes when solar energy is absorbed near the surface because of high concentrations of CDOM or phytoplankton (Mazumder and Taylor 1994; Fee et al. 1996). This effect of CDOM can explain the 1-m shallower location of the thermocline in Gribssø than Slotssø, which ensures a better light climate in the mixed surface layers than would occur in a deeper

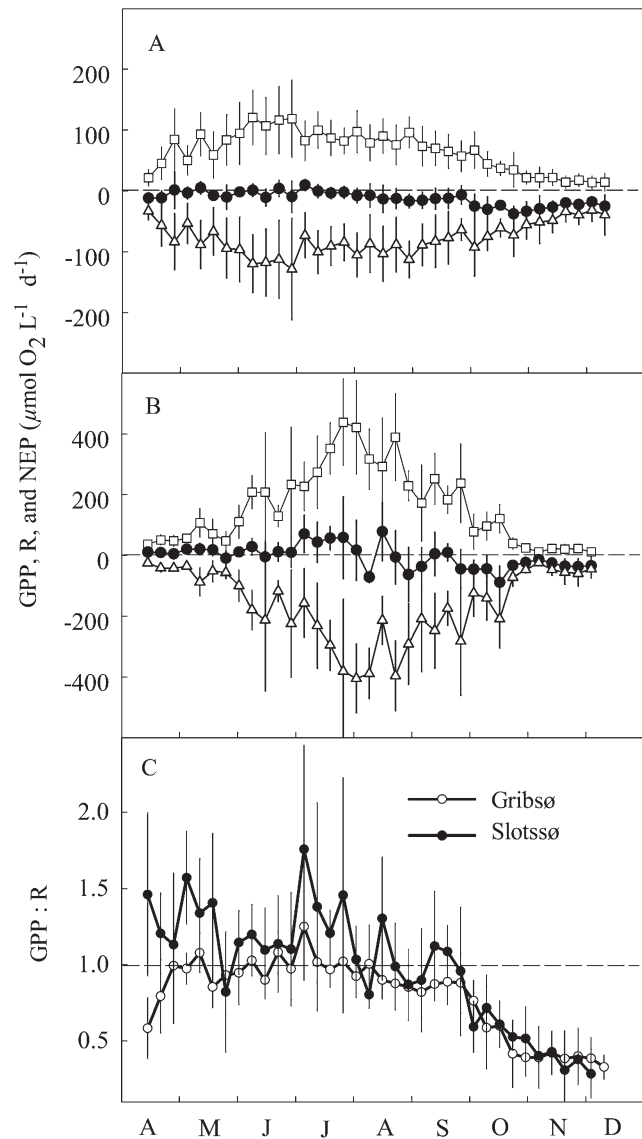


Fig. 4. Estimates of weekly values of gross primary production (GPP, open squares), net ecosystem production (NEP, closed circles), and community respiration (R , open triangles) as determined from continuous O_2 measurements in (A) Gribssø and (B) Slotssø from April to December 2006. Notice the different scales. R is presented as a negative number to facilitate plotting on the same graph as GPP. (C) The ratio between GPP: R is shown for weekly averages in both lakes. Negative values of NEP and GPP: R < 1 indicate periods where the lake consumes more oxygen in respiration than it produces in gross primary production.

mixed water column. Days of higher wind speed, deeper vertical mixing, and lower irradiances reduced GPP in both lakes (Table 3).

Ecosystem metabolism—Seasonal variability of GPP, R , and NEP was much more pronounced in Slotssø than Gribssø because higher and more variable nutrient input, higher phytoplankton biomass, and better light availability in the mixed layer in Slotssø enhance metabolic variability.

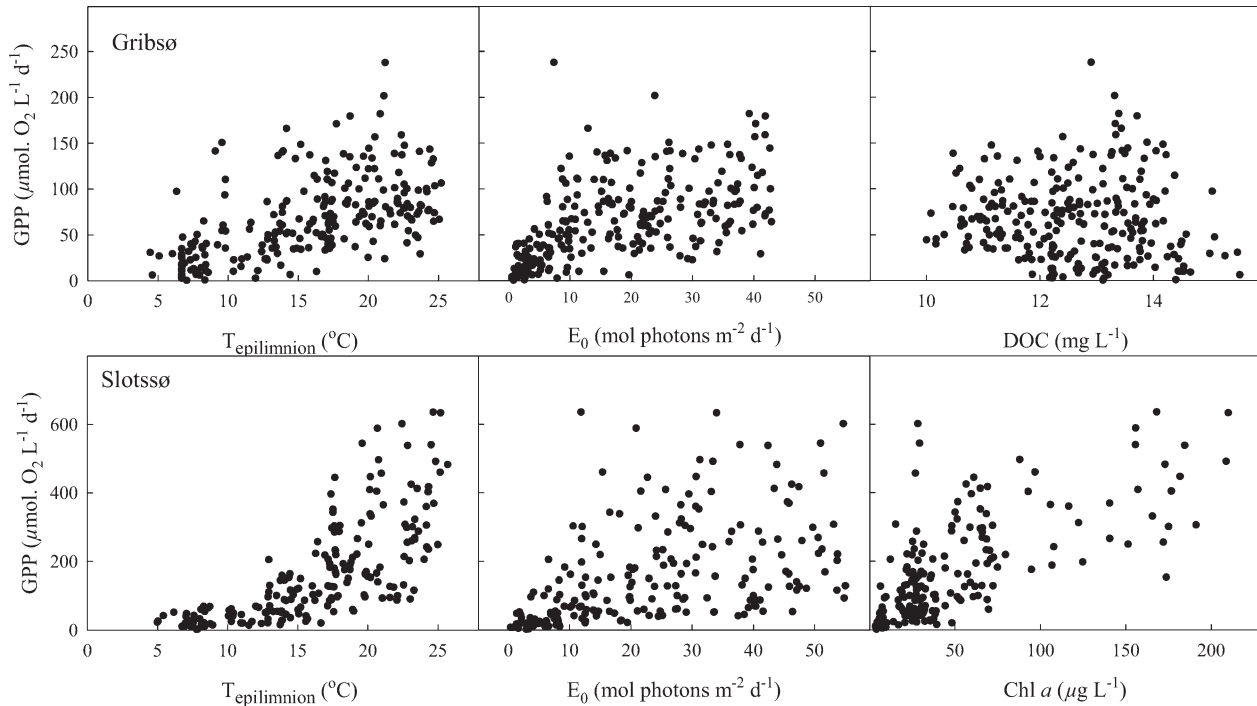


Fig. 5. Relationships between daily values of gross primary production (GPP), daily average values of water temperature in the epilimnion (T_{epi}), surface irradiance (E_0), dissolved organic carbon (DOC), and algal biomass (Chl a).

Accordingly, GPP was strongly dependent on the formation and collapse of algal blooms (Table 4). Metabolic rates in Slotssø resembled those previously measured (Staehr and Sand-Jensen 2007) with net autotrophy prevailing between mid-May and mid-September and net heterotrophy pre-

vailing for the rest of the year. Net autotrophy was anticipated for Slotssø during summer, since this is proposed to occur in nutrient-rich, CDOM-poor, and productive aquatic ecosystems at high irradiance (del Giorgio and Peters 1994; Schindler et al. 1997). Net

Table 4. Regression of GPP, R , and NEP ($\mu\text{mol O}_2 \text{ L}^{-1} \text{ d}^{-1}$) as a function of epilimnion temperature (T_{epi} , $^{\circ}\text{C}$), DOC (mg L^{-1}), mixing depth (Z_{mix} , m), daily mean irradiance (E_0 ; $\text{mol photons m}^{-2} \text{ d}^{-1}$), and Chl a ($\mu\text{g L}^{-1}$). The regression analysis was performed using the Autoreg procedure in SAS (SAS Institute 1994), which takes account of autocorrelated errors. Parameters are listed in order of decreasing importance, according to their t value. Only parameters that fulfilled a significance level of $p < 0.05$ are shown. Positive coefficients signify a positive effect on the dependent variable.

Lake	Dependent variable	Parameter	r^2	Coefficient	t	p
Gribssø $n = 244$	GPP	T_{epi}	0.83	1.93	3.74	0.0002
		DOC		3.70	3.10	0.0021
		Z_{mix}		-4.38	-3.08	0.0023
	R	E_0		0.70	2.82	0.0052
		T_{epi}	0.81	2.55	4.28	<0.0001
		DOC		4.40	3.52	0.0005
	NEP	Z_{mix}		-3.04	-2.08	0.04
		E_0	0.52	0.92	9.29	<0.0001
		DOC		-1.75	-8.91	<0.0001
Slotssø $n = 215$	GPP	T_{epi}	0.84	-0.47	-2.48	0.014
		Chl a		1.55	9.33	<0.0001
		T_{epi}		7.38	4.60	<0.0001
	R	DOC		-14.19	-4.12	<0.0001
		E_0		1.50	2.94	0.004
		Chl a	0.78	1.59	8.53	<0.0001
	NEP	T_{epi}		6.00	8.28	<0.0001
		E_0	0.23	1.77	5.61	<0.0001
		Z_{mix}		-4.76	-3.65	0.0003
		T_{epi}		-1.23	-1.69	0.05

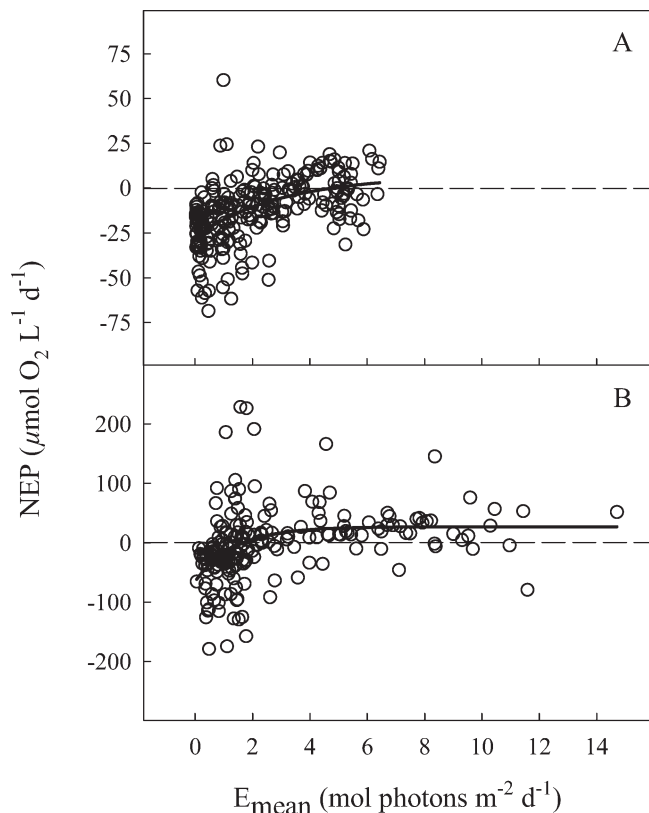


Fig. 6. Relationship between the daily mean available light level (E_{mean}) in the mixed surface layer and net ecosystem production (NEP) in (A) Gribssø and (B) Slotssø. Curves are fitted according to a nonlinear regression fit of NEP as a function of E_{mean} according to a saturating exponential model (Webb et al. 1974) modified for by including an offset (c at $E_{\text{mean}} = 0$): $\text{NEP} = \text{NEP}_{\text{max}} (1 - \exp(-\alpha E_{\text{mean}}/\text{NEP}_{\text{max}})) + c$, where α is the initial slope of the curve and NEP_{max} is the light-saturated net ecosystem photosynthetic rate. The offset (c) was incorporated to avoid the bias in the estimate of α that occurs when the curve is forced through the origin (Markager et al. 1999). The light compensation level (E_C) indicating the amount of light required for the mixed layer to attain autotrophy was determined as $E_C = \text{NEP}_{\text{max}} \log(1 + c/\text{NEP}_{\text{max}})/-\alpha$.

heterotrophy dominated in autumn following the collapse of phytoplankton blooms and mixing of the productive surface water with anoxic bottom waters (Fig. 4C).

Metabolic rates were threefold lower, less variable seasonally, and strongly heterotrophic in the dystrophic, DOC-rich Gribssø, having only a few summer days of net autotrophy. Accordingly, surface waters were usually undersaturated with oxygen at noon and day-to-day variability was very low (Fig. 1). Metabolism resembles that in other dystrophic lakes (Jonsson et al. 2001; Hanson et al. 2003). For Gribssø, a strong negative relationship existed between algal biomass (Chl a) and CDOM ($r = -0.64$, $p < 0.01$), suggesting that accumulation of humic matter depresses primary production, as observed for many small nutrient-poor lakes (Karlsson et al. 2009). This explanation is supported by predominant light absorption by CDOM (average 82%). Correcting for the shading effect

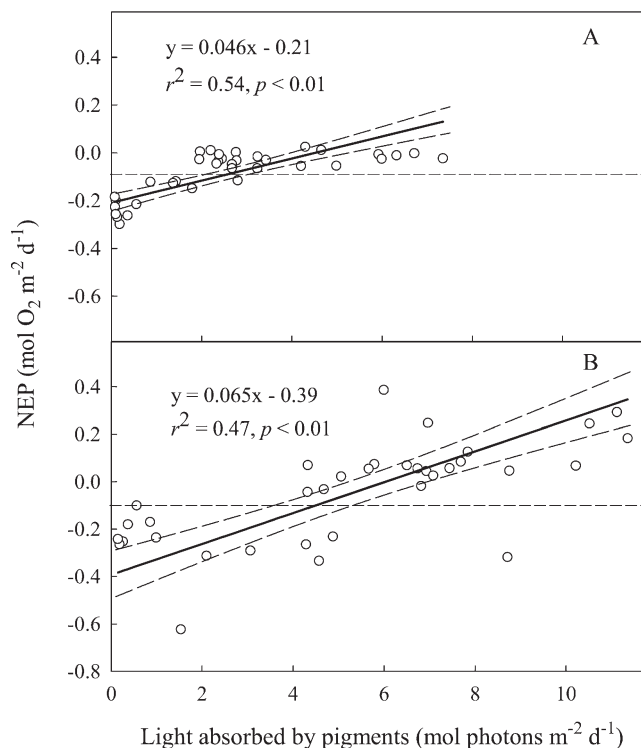


Fig. 7. Areal net ecosystem production (NEP) as a function of the daily incident irradiance absorbed by photosynthetic pigments in (A) Gribssø and (B) Slotssø. Curves are fitted using a geometric mean regression model, taking into account variability in both NEP and irradiance. Dashed lines represent the 95% confidence limits.

of CDOM on primary production, by determining NEP as a function of photon absorption by Chl a , showed that light dependence resembles each other in Gribssø and Slotssø (Fig. 7). Previous investigations on the effect of DOC on phytoplankton productivity (Jackson and Hecky 1980) showed that this results from a combination of elevated light attenuation, iron sequestering, and possibly phosphate sequestering directly by DOC, or indirectly through allocation of P to bacterial degradation of dissolved organic matter. The light attenuating effect by DOC is very strong in Gribssø (Fig. 3) and can alone account for most of the lower primary production compared to Slotssø.

Photons absorbed by photosynthetic pigments were used less efficiently in Gribssø (0.046 mol $\text{O}_2 \text{mol}^{-1}$ photons) than Slotssø (0.065 mol $\text{O}_2 \text{mol}^{-1}$ photons) based on NEP vs. photon absorption by pigments (Fig. 7). Assimilation numbers calculated as gross primary production per unit of chlorophyll in the surface layer also showed lower mean values (30%) in Gribssø than Slotssø. Nutrient deficient phytoplankton has lower photon efficiencies than nutrient-saturated phytoplankton (Staeher and Sand-Jensen 2006), and stronger nutrient limitation in Gribssø than Slotssø may, therefore, account for the observed differences. However, we cannot dismiss that inherent differences may exist between the phytoplankton communities of the two lakes being more photosynthetically active in Slotssø

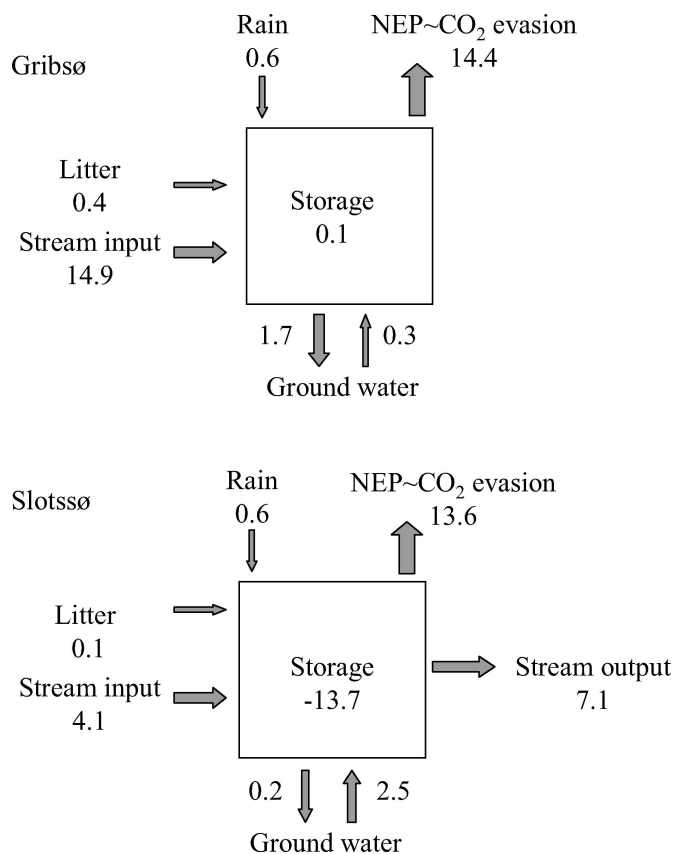


Fig. 8. Annual rates of carbon inputs, outputs, storage, and evasion ($\text{mol C m}^{-2} \text{ yr}^{-1}$) for Gribssø and Slotssø. Both lakes receive almost all carbon as TOC from streams, Gribssø significantly more so than Slotssø. While some of the imported carbon remains undegraded and becomes stored in Gribssø, the low net import of carbon in Slotssø is not sufficient to support the high respiration rates, which suggest a significant degradation of carbon stored in the lake sediments of Slotssø.

because of larger proportions of cyanobacteria, green algae, and centric diatoms in waters containing more nutrients and inorganic carbon.

Day-to-day variations in GPP and R were positively related to water temperature, while NEP decreased with temperature. This suggests a stronger temperature stimulation of R than GPP, which is expected because GPP is temperature dependent only at high saturating irradiances. Although the relationships of GPP and R to temperature appeared exponential, especially for Slotssø, this does not reflect a direct temperature influence on enzyme activity because the temperature dependency vanished when rates were normalized to chlorophyll (not shown). The linear relationship of GPP to surface irradiance reflects a strong and direct coupling, while the nonlinear saturating relationship between GPP and chlorophyll for Slotssø reflects the constraints on GPP of increasing self-shading of dense phytoplankton populations (Fig. 5). This is confirmed by the significant linear relationship of both GPP (not shown) and NEP to photon absorption of photosynthetic pigments (Fig. 7). The metabolic balance determined by NEP furthermore showed that both lakes changed from

net heterotrophy to net autotrophy with increasing irradiance, phytoplankton biomass (Chl a), low wind, and little mixing. These conditions caused higher mean irradiance in the mixed surface layer and higher light absorption by photosynthetic pigments, resulting in positive NEP values.

GPP and R followed each other over time in both lakes as reflected by NEP values near zero, GPP : R ratios near 1.0, and close positive correlations of daily GPP and R (Table 3). The implication of this finding is that most organic matter produced by photosynthesis is relatively rapidly respired by the same phytoplankton or by bacteria and zooplankton using the newly produced organic matter. During development of algal blooms in Slotssø, however, GPP : R ratios could reach about 1.5, and they were later followed by values of about 0.8 when the blooms collapsed and were degraded. As anticipated, the metabolic surplus during buildup of algal blooms in sunny, calm periods is faster and more distinct than the metabolic deficit during degradation of the algal blooms involving a greater suite of heterotrophic organisms over longer periods. In Gribssø, the variability was much less, and GPP : R ratios mostly ranged from 0.8 to 1.2 during spring and summer because there is little room for sudden rises of GPP with less nutrients and light being available.

During summer stratification, a small percentage of organic matter is lost to the hypolimnion. While part of this material is respired, most accumulates, either in the sediment or as DOC in the hypolimnetic water. Subsequently, when stratification vanishes in the autumn, the hypolimnion becomes reoxygenated and the accumulated reduced substances become reoxidized, resulting in elevated R and reduced NEP values. It appears that the duration of this enhanced R and lowered NEP following thermocline breakdown in October is short lived in both lakes (\sim a few weeks; Fig. 4). The effect of stratification on seasonal patterns in NEP and GPP : R are, however, not restricted to the autumn period. During summer stratification, sedimentation of dead phytoplankton into the hypolimnion causes a physical uncoupling of whole lake respiration, which is not reflected by diel oxygen variations in the epilimnion. In a previous study in Slotssø (Stæhr and Sand-Jensen 2007), we found that injections of oxygen-poor bottom waters could increase R and lower NEP. This effect was, however, only evident during periods with variable mixing depth in late summer. Reductions in mean light availability with increasing mixing depth will also reduce NEP and GPP. Seasonal changes in NEP and GPP : R would likely be less pronounced if development of the hypolimnetic oxygen deficit was currently included in daily budgets of NEP and R , although the integrated annual balance correctly reflects the lake processes.

Carbon balance—The annual carbon balance compares NEP calculated on a daily basis with long-term carbon inputs and outputs and infers carbon storage by difference. Daily NEP values can be biased by uncertainties in the calculated gas flux and input of oxygen-depleted water from external (stream and groundwater) or episodic internal (hypolimnion) sources. Relatively low wind speeds

in our study lakes (only a few days are above 4 m s^{-1}) suggest that gas exchange is a minor source of uncertainty. Also, relatively low external inputs of organic material and long water residence times of several months (Table 1) suggest that input of oxygen-depleted water is insignificant and that seasonal variations in NEP are primarily driven by internal processes rather than external loading. Furthermore, we use daily NEP to attain an integrated annual value (daily average NEP \times 365 d) for comparison with inputs and outputs to evaluate sinks and sources in the annual carbon balance. The estimated carbon budgets are sensitive to uncertainties in quantification of water fluxes and carbon concentrations. While water fluxes in Slotssø is dominated by input and output via streams, Gribsø is dominated by surface inflow and outflow to the groundwater, although a minor inflow of groundwater was measured in the northern part of the lake across from the outflow zone. To evaluate the reliability of our carbon budgets we performed a simple sensitivity analysis where the applied metabolic rates, water fluxes, and carbon concentrations were varied by $\pm 10\%$. This analysis showed only minor changes in the annual carbon budgets for both lakes, but especially Gribsø, was most sensitive to changes in stream TOC concentrations. These concentrations were either measured directly (Gribsø) or estimated from measurements of TP and C:TP quotients (Slotssø), giving acceptable confidence to the carbon budgets.

Both lakes, but especially Gribsø, were annually net heterotrophic. Allochthonous input of dissolved organic matter via small streams was the most important supplementary energy source to community respiration in Gribsø. Although allochthonous organic matter is more slowly degradable than autochthonous matter, the high quantities imported in dystrophic lakes have previously been found to dominate ecosystem metabolism (Wetzel 1992) and account for up to 80% of carbon mineralization (Jonsson et al. 2001). Low availability of inorganic nutrients and light to phytoplankton should further contribute to maintain the prevailing net heterotrophic state. In contrast, our mass balance indicates that excess respiration in Slotssø was fueled by sediment organic matter. Slotssø has been organically polluted for more than 350 yr (Christoffersen et al. 2004), and in the mid-1970s, Slotssø appeared to be annually net autotrophic (GPP:R = 1.6; Andersen et al. 1979) with high sedimentation rates of organic matter. Significant nutrient reduction of Slotssø commenced in 1990, and data from 2003 to 2008 show a decrease in phosphorus, nitrogen, and Chl *a*. Nonetheless, high algal abundance, high rates of primary production, and low import of allochthonous organic material should still push Slotssø toward net autotrophy. The overall mass balance, therefore, suggests that net heterotrophy in Slotssø derives from mineralization of easily degradable organic matter previously accumulated in the sediments. Recent reductions in external nutrient loading to Slotssø may have switched the lake from autotrophy to net heterotrophy.

In conclusion, we found large differences in light, nutrient, and mixing conditions between dystrophic Gribsø and eutrophic Slotssø. Nonetheless, both lakes were net heterotrophic but for different reasons, emphasizing the

importance of understanding historical as well as contemporary loadings for the present metabolic state. We found higher temporal variability in metabolism in eutrophic Slotssø, as a result of higher and more variable nutrient input, higher phytoplankton biomass, and better light availability in the mixed layer. GPP and R were tightly coupled in both lakes and strongly dependent on temperature. In accordance with Karlsson et al. (2009), we found that primary production was light limited in both lakes but, in addition, nutrient limited for long periods in Gribsø and for short periods in Slotssø. Greater absorption by CDOM in the forest lake competitively inhibits photosynthesis of phytoplankton such that higher incident irradiances are needed for photosynthesis to balance community respiration, compared to the phytoplankton dominated eutrophic lake. Thus, our study does not support the simplistic view that dystrophic and eutrophic lakes represent two alternative stable states, which function fundamentally differently. Rather our study supports Carpenter and Pace's (1997) idea that distinct differences in inputs of nutrients and organic matter, either historical or contemporary, determine the present lake trophic status and strongly affect the magnitude and variability in lake metabolism through changes in the relative importance of different drivers.

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