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Temporal dynamics and regulation of lake metabolism

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Abstract

We studied temporal dynamics and regulation of oxygen metabolism in the upper mixed layer of a nutrient-rich shallow Danish lake by continuous measurements of oxygen, irradiance, wind, and temperature and frequent measurements of algal chlorophyll, organic pools, and inorganic nutrients. Chlorophyll, algal growth rate, and mean irradiance (E_{mean}) in the mixed surface layer were calculated daily from continuous measurements of irradiance and temperature with depth. There were three to four distinct maxima in gross primary production (GPP) and community respiration (R) during the summer season and minima from fall to spring after broad-scale changes in irradiance, temperature, mixing depth, and biomass and growth rate of the algal community and concentrations of inorganic nutrients. Lake metabolism was annually balanced (mean GPP : R 1.04 in 2003 and 1.01 in 2004), with net autotrophy occurring mainly from mid-May to mid-September (mean GPP : R 1.14 in 2003 and 1.10 in 2004), and net heterotrophy outside this period (mean GPP : R 0.60 in 2003 and 0.81 in 2004). However, GPP : R varied two- to threefold from day to day because lower surface irradiance, higher mixing depth, and thus lower E_{mean} significantly reduced GPP. Normalizing GPP to chlorophyll provided an index of algal growth potential (GPP^B), which followed a hyperbolic relationship to E_{mean}, and both parameters were related to blooms and collapses of algal biomass. Metabolic rates were much more variable from day to day than algal biomass, which integrates growth and loss processes over longer periods. The continuous approach to lake metabolism provides better data and can provide a more accurate picture than averages of a few discrete measurements. Weekly averages reflected the characteristic seasonal peaks and troughs also observed for algal biomass, whereas monthly averages did not. Daily measurements of lake metabolism, therefore, can provide the optimal background for evaluating temporal changes and regulation of algal biomass and organic pools in nutrient-rich shallow lakes.

Gross primary production, ecosystem respiration, and the balance between the two are known to vary widely across aquatic ecosystems and to display large temporal variations within ecosystems (D'Avanzo et al. 1996; Smith and Hollibaugh 1997; Cole et al. 2000). Although intersystem differences and long-term changes in annual and seasonal patterns have been studied for several decades (e.g., Odum and Hoskins 1958; Whittaker and Likens 1973), much less is known of the considerable short-term changes in metabolism between days and weeks. Day-to-day differences in irradiance and temperature obviously affect rates of photosynthesis and community respiration, and weaken statistical relationships to nutrients and biomasses of phytoplankton, bacteria, and zooplankton. Despite the highly dynamic behavior, many previous studies of lake metabolism have been forced to use time-averaged conditions for years and seasons rather than the dynamic daily values (Kalff 2002), which can now be monitored by new, reliable, and fairly cheap technologies. The improved understanding of temporal dynamics obtained by a continuous monitoring approach therefore has the potential to strengthen predictions of how changes in environmental conditions (e.g., climate, deforestation, eutrophication) affect metabolic rates of a specific ecosystem. This study was initiated to investigate this potential by attaining a high temporal resolution of ecosystem metabolism and the regulating physical, chemical, and biological parameters.

A variety of techniques have been used to measure metabolic rates in aquatic ecosystems. Howard T. Odum was the first to develop a method of calculating metabolic rates from diel fluctuations of oxygen concentrations in the free-moving water of streams (Odum 1956; Odum and Hoskins 1958). Since then, the oxygen mass balance method has been applied in many studies of streams, but estuaries and lakes have been examined too (e.g., Markager and Sand-Jensen 1989; D'Avanzo et al. 1996; Cole et al. 2000). The method relies on the fact that changes in oxygen concentration reflect the biological balance between plant photosynthesis and ecosystem respiration, and the physical exchange of oxygen between air and water. Ecosystem gross primary production (GPP) is defined as the assimilation of inorganic carbon into organic plant material and oxygen release through photosynthesis. Total ecosystem respiration (R), in contrast, is the release of CO_2 and uptake of oxygen caused by aerobic degradation of organic material by all organisms and the oxidation of reduced compounds (e.g., Fe^{2+} and S^{2-}) formed by anaerobic respiration.

The balance between GPP and R, determined either as the gross production/respiration ratio (GPP : R) or the net ecosystem production (NEP = GPP − R), is a measure of trophic status of an ecosystem (Odum 1956) and the

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availability of autochthonous organic matter for harvest and export to adjacent regions (Fisher and Likens 1973; Kemp et al. 1997; Smith and Hollibaugh 1997). Permanently net autotrophic systems or periods with net autotrophy within systems (GPP : R $>$ 1, NEP $>$ 0) can support an export of organic material from the ecosystems and/or accumulation of organic material within the ecosystem. Net heterotrophic systems or periods (GPP : R $<$ 1, NEP $<$ 0), in contrast, require import of organic material from outside or net degradation of organic pools accumulated within the system's boundaries. On a global scale, GPP : R and NEP are useful for 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).

Significant diel oscillations in GPP, NEP, and GPP : R take place in ecosystems as a response to the diurnal light cycle. As most autotrophic organisms in lake ecosystems live longer than a day, variations in irradiance between days and weeks will also be important for variations in ecosystem metabolism on these temporal scales. Variations in metabolism over longer timescales of 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 be a response to ecosystem succession, eutrophication, invasion of new species and climate change. Nutrient enrichment, for example, has been found to push lakes from net heterotrophy to net autotrophy by stimulating GPP more than R (del Giorgio and Peters 1994; Schindler et al. 1997; del Giorgio et al. 1999). Greater inputs of dissolved organic matter stimulate R and may even reduce photosynthesis because of greater background light attenuation in the water column and, thereby, lead to net heterotrophy (del Giorgio and Peters 1994; Krause-Jensen and Sand-Jensen 1998). Ecosystem metabolism is also sensitive to changes in food web structure influencing algal biomass and GPP (Schindler et al. 1997; Pace and Cole 2000).

This study was motivated by the apparent lack of empirical relations on the physical, chemical, and biological drivers of short-term variability in lake metabolism. The overall aim was to investigate the dynamic behavior and environmental control of lake metabolism. On the basis of 2-yr data on oxygen mass balance, temperature, irradiance, stratification depth, light attenuation, chlorophyll *a* (Chl *a*), organic matter, and inorganic nutrients, we evaluated two specific properties: the importance of major physiochemical and biological parameters for variations in ecosystem metabolism, and the temporal variability in ecosystem metabolism.

Materials and methods

Study site—The study was conducted from May 2003 to November 2004 in Frederiksborg Slotssø, a small (0.22 km^2), shallow (Z_{mean} = 3.5 m, Z_{max} = 8 m), dimitic, and highly productive lake located on Zealand (56°N, 12°E), Denmark (Andersen and Jacobsen 1979, Christoffersen et al. 1990, 1993). The lake is surrounded by steep banks and lacks a normal littoral zone and submerged plants because only 2% of the bottom areas are shallower than 1 m. During summer stratification, the well-mixed surface waters where oxygen measurements are conducted include approximately 75% of the water volume and are in contact with 80% of the lake bottom. These conditions make the lake relatively well suited for estimating budgets of lake metabolism, because the input of organic material from land and the littoral zone is small (~5%) and the respiratory processes in the hypolimnion are much smaller than those in the relatively well-mixed pelagic waters (Andersen and Jacobsen 1979).

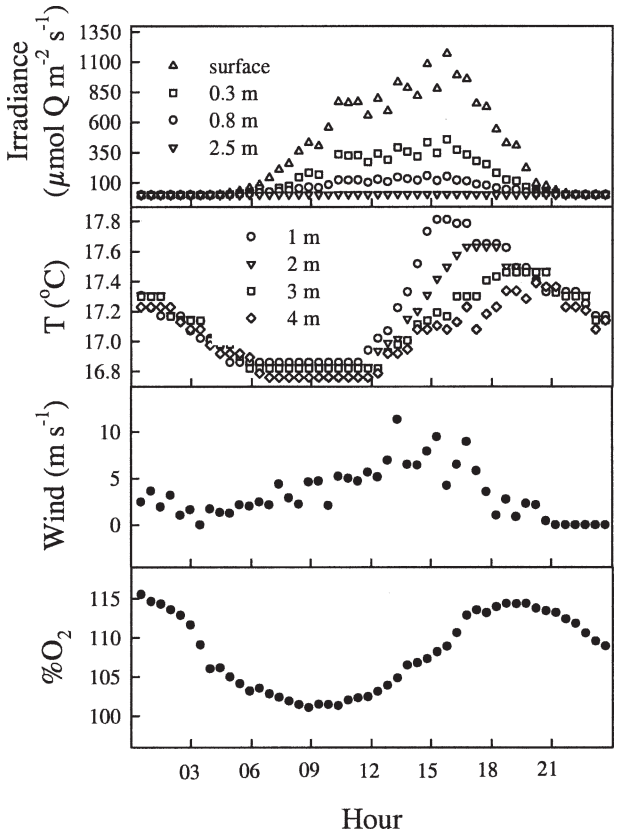

Fig. 1. Example of continuous measurements of irradiance, temperature, wind speed, and oxygen saturation in Frederiksborg Slotssø on 30 June 2004.

Monitoring station—Continuous measurements of oxygen concentration, wind speed, temperature, and irradiance in air and at different depths in the water were performed at the center of the lake with sensors mounted on a floating raft (Fig. 1; Table 1). No measurements were performed during winter ice cover (December 2003 to February 2004). Oxygen and irradiance sensors were cleaned every week during summer (May to September) and every two weeks outside this period. On the same occasions, the oxygen electrode was removed for calibration (0% and 100% air saturation at the ambient water temperature), and data were retrieved from the data loggers. Drift of oxygen sensors between calibration and cleaning was negligible.

Table 1. Parameters recorded by the monitoring station from May 2003 to November 2004 in Frederiksborg Slotssø and specifications regarding instruments and frequency and locations of measurements.

Parameter	Sonde	Data logger	Frequency	Depth (m)
$\%O_2$	Global water (May 03 to Dec 03) Oxyguard (Dec 03 to Nov 04)	Global water	10 min	−0.5
Wind speed	Global water	Global water	10 min	+1.0
Temperature	Stowaway tidbit		10 min	+0.2, −0.5, −1, −2, −3, −4, −5, −6, −7
Irradiance	LiCor 2π quantum sensor	LiCor 1000	30 min	+1.0, −0.3, −0.8, −2.5

Profiles and water sampling—To test further the homogeneity of the water column, depth profiles of oxygen concentration, pH, and temperature were recorded with an YSI 600XL multisonde at every visit to the monitoring station. Water was collected from the upper mixed water column to determine ionic strength and alkalinity and concentrations of Chl *a*, dissolved organic matter, total suspended matter, and inorganic nutrients.

Water analysis—Samples for Chl *a* and pheopigments were filtered through Advantec GC-50 filters, extracted with 96% ethanol for 24 h, and measured according to the method described by Parsons et al. (1984) with a Shimadzu UV-160A spectrophotometer. Dissolved organic matter (DOM) was quantified as the absorbance of colored DOM (CDOM) by measuring the absorbance of a GF/F filtrate (0.7 μm) at 380 nm through a 5-cm cuvette in the spectrophotometer. Samples for total suspended matter (TSM) were filtered through precombusted GF/F filters and dried at 60°C for 24 h. TSM was calculated as the weight difference. To determine the concentration of inorganic nitrogen ($NO_3^- + NH_4^+$) and inorganic dissolved phosphorous (PO_4^{3-}), 20-mL samples were filtered through a GF/F filter and stored in acid-cleaned plastic vials at −18°C until analysis. Nitrate was quantified with a rapid Flow Analyzer Alpkem (ALPKEM 1990), ammonia was determined according to Solórzano (1969), and phosphate and silica were determined according to Strickland and Parsons (1968). Dissolved inorganic carbon was calculated from temperature, ionic strength, pH, and alkalinity according to Eaton et al. (1995).

Oxygen flux—Electrode recordings of oxygen concentrations every 10 min (Table 1) were used to calculate NEP for 30-min intervals according to the following equation formulated by Cole et al. (2000): $NEP_{30\ min} = \Delta O_2 - D/Z_{mix}$, where ΔO_2 is the change in oxygen concentration over 30 min, D is the diffusive exchange with the atmosphere in this period, and Z_{mix} the mixing depth. Diffusion was calculated as $D = k\ (O_2 - O_{2sat})$, where O_{2sat} is the concentration of oxygen in equilibrium with the atmosphere and k is the coefficient of gas exchange of oxygen at a given temperature. k_{600} (k for a Schmidt number of 600) was estimated as a function of wind speed at 10 m above the lake by the equation of Cole and Caraco (1998). Assuming a neutrally stable boundary layer, wind speed at 10 m was calculated from our measurements at 1 m by using the empirical relationship described in Smith (1985). The coefficient of oxygen exchange, k, was calculated for each temperature from the estimate of k_{600} and the ratio of Schmidt numbers according to Jahne et al. (1987). Summing the 48 $NEP_{30\ min}$ values found over a 24-h period gave a daily value called NEP_{daily}. Calculations of $NEP_{30\ min}$ during night divided by the time length (h) provided the hourly rate of ecosystem respiration during night (R_{night}). Assuming the same respiration rate took place during night and day, we multiplied the hourly rates by 24 h to attain the daily respiration (R_{daily}). This allowed us to calculate gross daily primary production (GPP) as $NEP_{daily} + R_{daily}$. Daily estimates of Chl *a* specific gross primary production (GPP^B) was finally calculated by dividing GPP with daily estimates of Chl *a* (*see below*).

Mixing depth—Daily estimates of water mixing depth (Z_{mix}) were determined to evaluate the effect of water column stratification on the calculated gas flux. Z_{mix} was determined every day from continuous temperature readings at eight depths (Table 1). Stratification of the water column was defined when the temperature gradient exceeded 1°C m^{-1}. According to this definition, stratification was found at more than one depth interval on several days. However, because gas flux measurements were determined at 0.5-m depth, we only considered the uppermost stratification depth.

Light attenuation and light availability—The vertical light attenuation coefficient of photosynthetically available light (K_d, 400–700 nm) was determined as the slope of a linear regression model of irradiance (E_z) versus depth (z) as $\ln(E_z) = b + K_d z$. Continuous irradiance recordings allowed 10–24 models of K_d to be determined each day between sunrise and sunset. Only models with $r^2 > 0.8$ were accepted when computing the daily average K_d values. Fouling of the underwater light sensors occurred during the productive summer periods. The comparison of pre- and postcleaning values, however, only caused minor increases in the calculated K_d because sensors at different depths became almost equally fouled with time. Days with increased K_d values as a result of fouling occurred less than 5% of the time, and these data were removed from the further analysis.

Available light—Daily light availability (E_{mean}; mol photons $m^{-2}\ d^{-1}$) for the algae was calculated as an average for the surface mixed zone. By using data for daily surface irradiance (E_0; mol photons $m^{-2}\ d^{-1}$), mixing depth (Z_{mix};

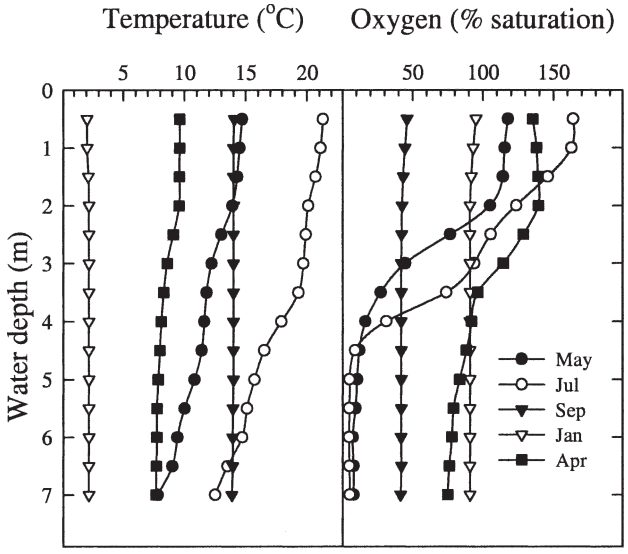

Fig. 2. Representative profiles of temperature and O_2 and for spring, summer, and fall in the lake.

m), and light attenuation (K_d; m^{-1}), with a constant of 0.1 selected for backscattering and surface reflection, β (Kirk 1994), the following equation was modified from Riley (1957): $E_{mean} = E_0(1 - \beta)\ (1 - e^{-K_d Z_{mix}})/(K_d Z_{mix})$.

Continuous chlorophyll estimates—Multiple linear regression analysis of K_d as a function of Chl *a*, CDOM, and TSM showed that the variation in K_d was primarily controlled by algal concentration because CDOM did not add significantly to the model fit and TSM as a result of a high intercorrelation with Chl *a* ($r^2 = 0.87$), only raised r^2 by an average of 3% in the multiple regression model. The relationship between Chl *a* (μg Chl *a* L^{-1}) and K_d (m^{-1}) followed a power function: Chl $a = 4.0 + 3.36\ e^{1.25}\ K_d$. Applying the power function on daily measurements of K_d allowed daily estimates of Chl *a*. These estimates were furthermore used to calculate the specific phytoplankton community growth rate (μ) over subsequent periods of 2 d: μ (d^{-1}) = (ln B_2—ln B_0)/days, where B_2 and B_0 represent the algal biomass (Chl *a*) the day before and after the growth period, respectively.

Results

Physical and chemical changes—The water column was stratified from mid-May to mid-September (Figs. 2 and 3A). Stratification commenced when surface temperatures exceeded ~8°C and persisted until temperatures fell below ~15°C. During stratification variations in Z_{mix} were closely related to temporal changes in surface temperature, whereas wind speed (95% of the time below 5 m s^{-1}) had little influence (Table 2). Stratification of the water column resulted in low oxygen concentrations in the hypolimnion (Fig. 3D) and depletion of inorganic carbon and nutrients in the epilimnion (Fig. 4A,B). By using half-saturation constants for uptake of N (~2.5 μmol L^{-1}; Eppley et al. 1969), P (~0.2 μmol L^{-1}; Furnas et al. 1976), and Si (~2.5 μmol L^{-1}; Azam and Chisholm 1976), we found several periods during spring and summer with potential nutrient limitation of phytoplankton growth (Fig. 4A).

Organic matter and algal growth—The concentration of CDOM varied little over time, but higher concentrations developed during spring and summer and concentrations fell during autumn and winter (Fig. 4C). Strong seasonal changes, however, occurred in phytoplankton biomass, algal growth rate (Fig. 4D), and in TSM (Fig. 4C). The high temporal resolution of Chl *a* determined from continuous measurements of light attenuation revealed several peaks in phytoplankton abundance and growth rate during the growth season. The negative relation between algal biomass and growth rate (Table 2) is due to a time lag between growth rate and biomass accumulation of approximately one week. Correcting for this time difference revealed a positive relation between algal growth and biomass accumulation ($r = 0.39$, $p < 0.0001$). Blooms of diatoms in spring and fall were accompanied by marked depletion of silica (Fig. 4A). High algal biomass resulted in low concentrations of inorganic nutrients during long periods of water column stratification. Particularly high biomass of blue-green algae (i.e., species of *Microcystis* and *Anabaena*) developed in late summer at high temperature and low mixing depth (Fig. 3A and 4D). The fast formation of the summer bloom was accompanied by a threefold decline of dissolved inorganic carbon (DIC) concentrations because carbon was incorporated in plankton organisms and $CaCO_3$ precipitated at high pH. This phenomenon was reflected by a parallel rise of chlorophyll and suspended matter and loss of degradable organic matter to the hypolimnion and by oxygen depletion there (Fig. 3D and 4C, D). The decline of DIC during formation of the summer bloom in 2003 amounted to ~1.6 mmol L^{-1} or 15.4 mg C L^{-1}. The parallel rise in algal biomass (ca. 200 μg Chl *a* L^{-1}) corresponded to about 10 mg C L^{-1} for a C : Chl ratio of 50 and the rise of suspended organic matter corresponded to 11.7 mg C L^{-1} for a C : TSM ratio of 0.45. Gradual degradation of the plankton blooms and dissolution of $CaCO_3$ reestablished the DIC pool suggesting that net autotrophy during establishment of the phytoplankton blooms and the oxygen depleted hypolimnion was followed by net heterotrophy when the organic pools degraded and the hypolimnion was reoxygenated (Fig. 4A, D).

Temporal pattern in ecosystem metabolism—Rates of GPP, NEP, and R increased during spring, reached a maximum in late summer and declined in fall and winter (Fig. 5). Annual rates of GPP were 123 ± 10 SE μmol O_2 L^{-1} d^{-1} in 2003 and 86 ± 6 SE μmol O_2 L^{-1} d^{-1} in 2004. The lake was net autotrophic with annual average NEP values of 4.5 ± 8 SE μmol O_2 L^{-1} d^{-1} in 2003 and 0.8 ± 3.9 SE μmol O_2 L^{-1} d^{-1} in 2004 (*see also* Fig. 6). Days of net heterotrophy occurred during all months, but were most frequent during autumn and winter between October and April (Fig. 5B) when mean NEP values were significantly below 0 at −37 ± 6 SE μmol O_2 L^{-1} d^{-1} in 2003 and −11 ± 2 SE μmol O_2 L^{-1} d^{-1} in 2004.

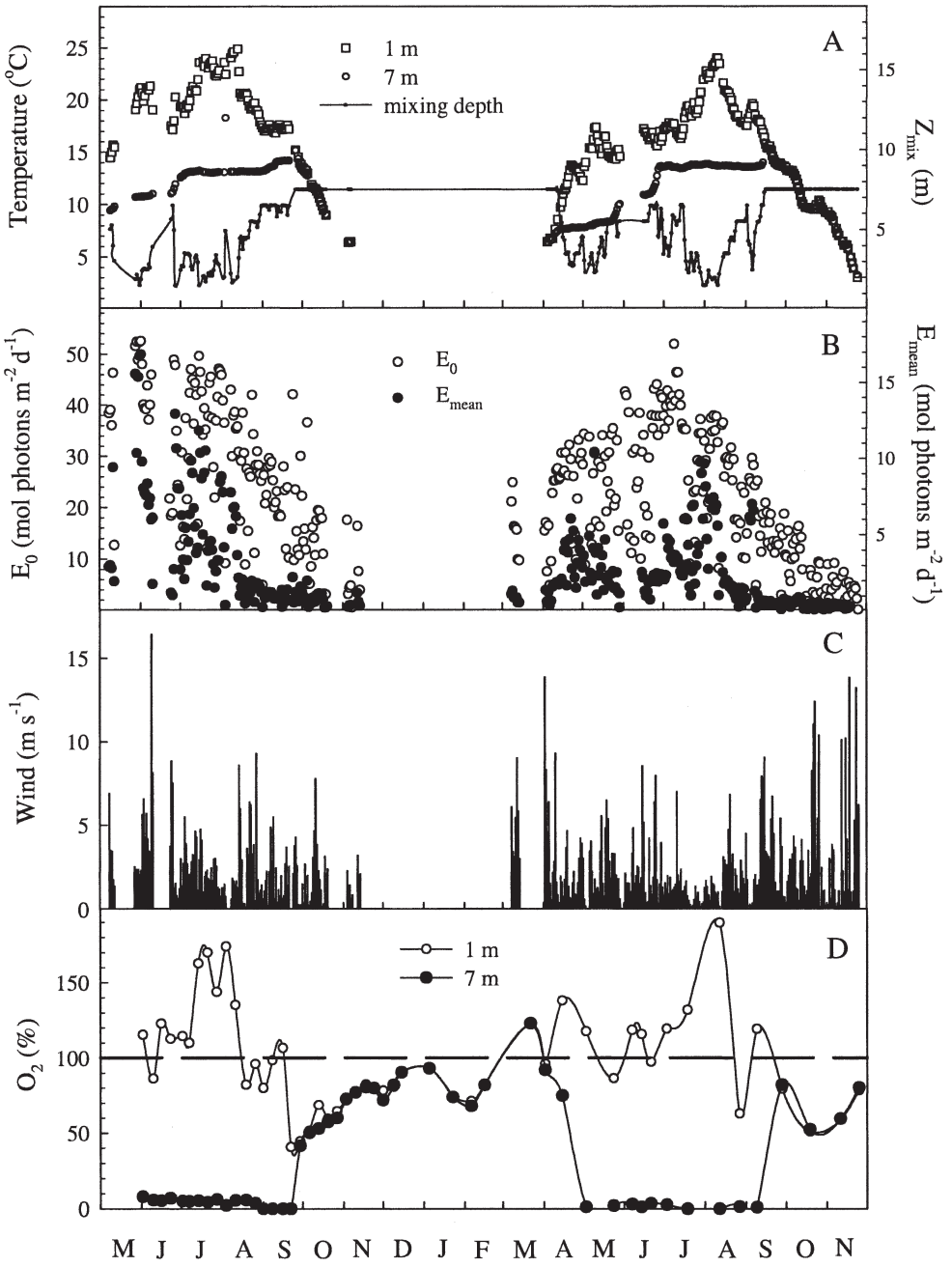

Fig. 3. Seasonal changes in daily water temperature, calculated mixing depth (Z_{mix}), surface irradiance (E_0), mean irradiance (E_{mean}) in mixed surface layer, wind speed calculated at 10 m above lake surface, and weekly measurements of oxygen saturation in surface and bottom water.

Large day-to-day variations in GPP, NEP, R, and GPP : R mirrored the rather stochastic metabolic behavior of the studied lake. Daily variations in GPP, NEP and R were significantly smoothed by averaging values on a weekly basis and smoothed even further when averaged over a month (Fig. 6). The apparently less variable rates of GPP at longer timescales, however, were accompanied by a significant increase in the variability of the estimated mean rates. Thus, the coefficient of variation (CV = $SD/\bar{X}$ × 100%) was lower within weeks (55%) than between months (61%) or years (87%) for GPP. The standard deviation of weekly and monthly averages of GPP increased linearly with the mean value ($r^2 = 0.70$, $p < 0.001$). Consequently, highly productive periods such as August, with large day-to-day variations required more sampling days to obtain a representative measure of the monthly mean value compared to periods such as November with a low and more constant metabolism (Fig. 7).

Regulation of ecosystem metabolism—Rates of GPP and NEP were strongly stimulated by increasing temperature,

Table 2. Pearson correlation coefficients between daily estimates of gross (GPP) and net (NEP) ecosystem production, respiration (R), autotrophy/heterotrophy (GPP : R), algal growth rate (μ), temperature (T) at 0.5 m depth, daily surface irradiance (E_0), daily mean irradiance (E_{mean}) in mixed surface waters, mean wind speed at 10 m above surface, mixing depth (Z_{mix}) and algal biomass (Chl *a*).

	NEP	R	GPP : R	μ	T	E_0	E_{mean}	Wind	Z_{mix}	Chl *a*
GPP	0.59***	0.69***	0.43***	0.11*	0.54***	0.42***	0.23***	−0.20**	−0.35***	0.44***
NEP		−0.18**	0.73***	0.27***	0.32***	0.45***	0.48***	−0.26***	−0.42***	0.04
R			−0.13*	−0.11*	0.37***	0.12*	−0.15**	−0.01	−0.04	0.50***
GPP : R				0.29***	0.52***	0.53***	0.60***	−0.18**	−0.55***	0.11*
μ					0.23***	0.13*	0.41***	−0.17**	−0.43***	−0.43***
T						0.60***	0.51***	−0.02	−0.74***	0.45***
E_0							0.75***	0.03	−0.58***	0.12*
E_{mean}								−0.04	−0.76***	−0.18**
Wind									0.12*	0.15**
Z_{mix}										−0.03

*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$, $n = 303$.

surface irradiance and algal biomass (only GPP, Table 2) reflecting the contrasts between high rates from mid-May to mid-September and low rates outside this period. Metabolic rates were, however, negatively related to increasing mixing depth as a result of both the seasonal contrasts between winter of deep mixing and summer of limited mixing and the constraints on GPP and subsequently on NEP caused by the lower E_{mean} value accompanying deeper vertical mixing (Table 2). The level of autotrophy (GPP : R > 1 and NEP > 0) increased significantly with algal growth rate, which also responded positively to mean irradiance and temperature but negatively to increasing mixing depth.

Although the relationships of GPP and NEP to temperature appear exponential (Fig. 8), this does not directly reflect a temperature influence on enzyme activities because it vanishes when rates are normalized to chlorophyll. The rather linear relationship of GPP and NEP to surface irradiance reflect a strong and direct coupling, whereas the saturating relationship to chlorophyll reflect the constraints of increasing self-shading. The correlation between GPP and R (Table 2) was anticipated as respiratory processes utilize the organic compounds originally produced by photosynthesis. The significant seasonal variations in the GPP : R ratio (Fig. 5C), however, suggest that respiration is fueled not only by organic material from photosynthesis. Periods with high respiration and low productivity (i.e., low GPP : R ratio) during autumn and winter coincide with collapse of water column stratification. Increased respiration rates in these periods were therefore most likely fueled by organic material accumulated in the epilimnion. The metabolic balance determined by NEP and GPP : R furthermore showed that the lake changed from net heterotrophy to net autotrophy with increasing temperature and surface irradiance, while increasing mixing depth made the lake more heterotrophic (Fig. 8 and Table 2). The relationship of algal biomass to NEP and GPP : R was weak and inconsistent.

A stepwise multiple regression model that used all of the available data showed that temperature was the overall best predictor of daily values of GPP, whereas changes in algal biomass accounted for most of the daily variability in respiration rates (Table 3). Strong correlations between GPP and algal biomass (Table 2), especially during summer (Table 3), however, indicate that daily changes in algal biomass were an important driver of both GPP and R. The daily metabolic balances determined as either NEP or GPP : R were both strongly related to variations in mixing depth and only responded weakly to changes in surface irradiance, temperature and wind conditions. For all metabolic parameters, more variability was accounted for when moving from daily, over weekly to monthly scales. Coefficients of determination for GPP were accordingly much higher for models based on monthly ($r^2 = 0.93$) rather than weekly ($r^2 = 0.77$) or daily data ($r^2 = 0.44$). The stepwise multiple regression analysis was also performed on data for spring (March to May), summer (June to August), and fall (September to November). This division of data showed an increased ability of surface irradiance to account for variations of GPP and NEP, and revealed a stronger coupling to environmental variables and rates of GPP and NEP during the relatively low productive spring and fall periods, than during the highly productive and variable summer period (Table 3).

Normalizing metabolic rates to chlorophyll *a* resulted in a close relationship of GPP^B to irradiance. In particular, the relationship of GPP^B and NEP^B to mean irradiance in the mixed surface waters (E_{mean}) followed a close hyperbolic relationship (Fig. 9) with r^2 values of 0.34 (GPP^B) and 0.37 (NEP^B). The calculated mean saturation irradiance (E_k) was lower for GPP^B than for NEP^B (5.5 and 7.5 mol photons m^{-2} d^{-1} respectively) and the mean light compensation level (E_C) for NEP^B was 2.3 mol photons m^{-2} d^{-1}.

Stepwise multiple linear regressions on the residual between modelled and measured values of GPP^B revealed a significant negative relationship to wind velocity (r^2 of 7%) and mixing depth (r^2 of 6%). A similar analysis of the residuals of NEP^B showed a significant negative relationship to wind velocity (r^2 of 4%). Furthermore, GPP^B was positively related to growth rate of the algal community (μ) when applying a lag phase of 3 d between GPP^B and μ (r =

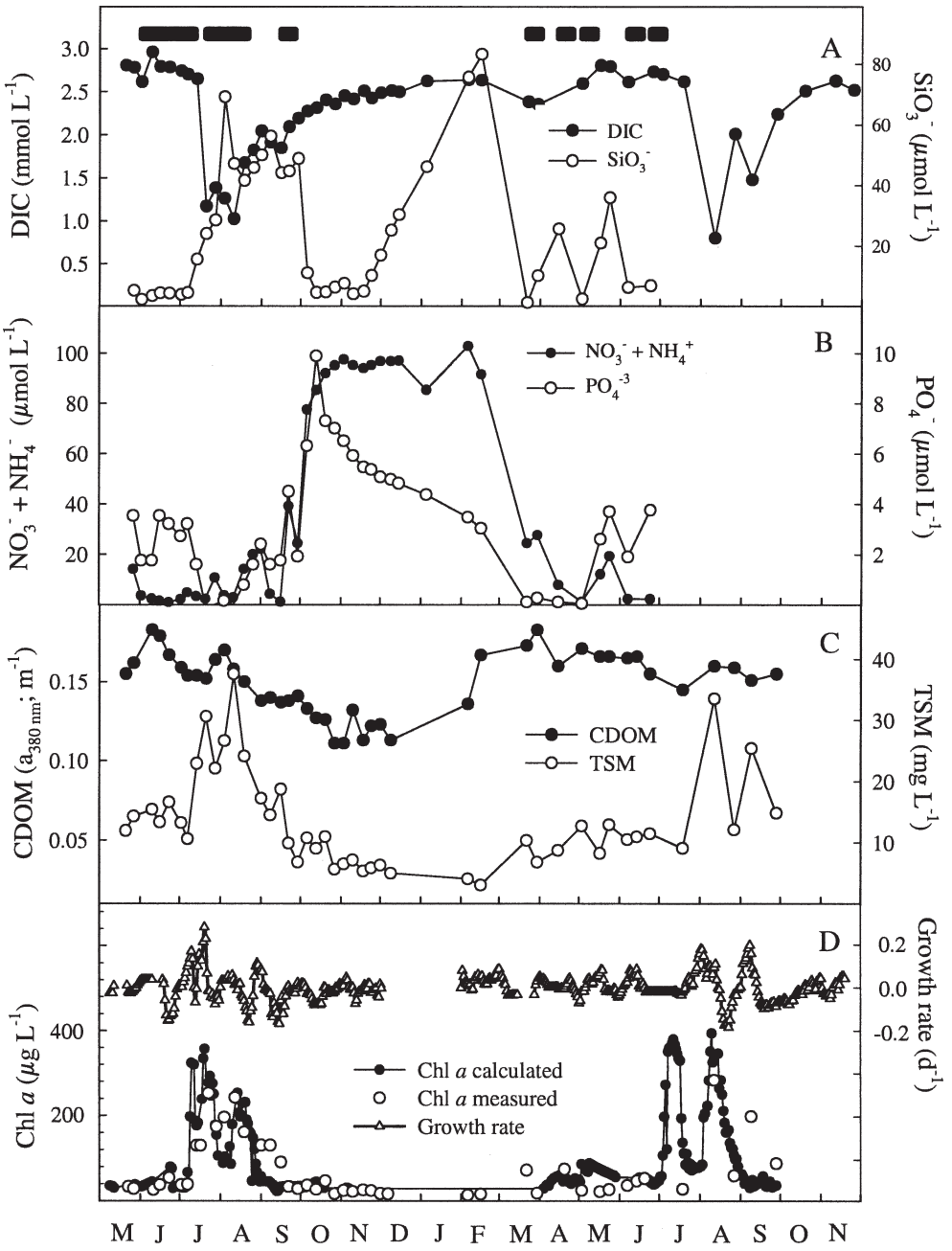

Fig. 4. Seasonal changes in concentrations of inorganic nutrients, dissolved and particulate organic material, Chl *a*, and algal specific growth rate in Frederiksborg Slotssø. Periods of potential nutrient limitation for algal growth (horizontal bars in (A)) were designated when concentrations of N, P, or Si fell below their respective half-saturation constants.

0.48, $p < 0.001$, data not shown), suggesting GPP^B to be a useful determinant of algal growth potential.

Discussion

Annual and seasonal patterns of ecosystem metabolism—Our calculations of ecosystem metabolism from continuous oxygen measurements showed large variations in GPP, R, NEP, and GPP : R on a daily basis, across seasons, and between succeeding years. Rates of GPP and R resembled those previously obtained by bimonthly bottle measurements in Frederiksborg Slotssø (Andersen 1978), reaching the highest GPP levels in August (about 250 μmol O_2 L d^{-1} in our and 190 μmol O_2 L d^{-1} in Andersen's study) and displaying similarly low GPP values in winter (5–10 μmol O_2 L d^{-1} in our and 4 μmol O_2 L d^{-1} in Andersen's study). We found the lake to be predominantly net autotrophic between mid-May and mid-September and for the year as a whole, also in accordance with Andersen's many fewer measurements. Net autotrophy was anticipated for Freder-

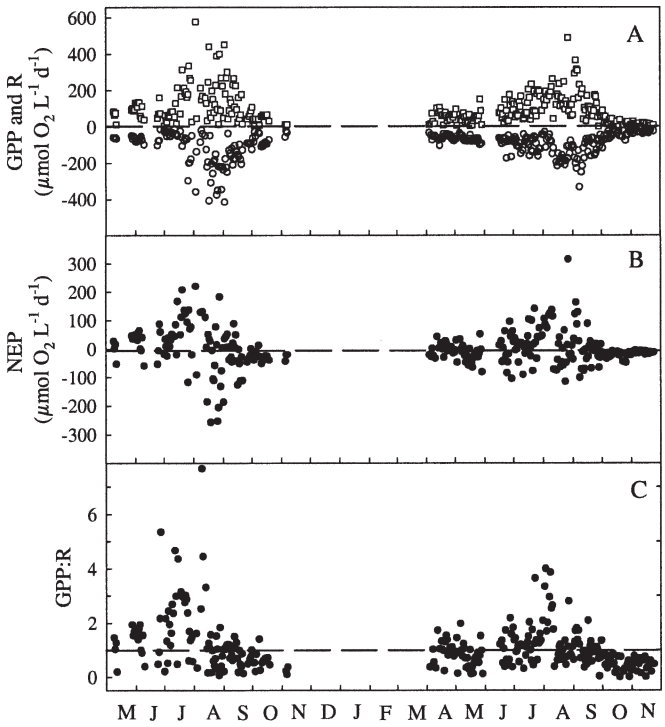

Fig. 5. Daily estimates of (A) gross primary production (GPP, open squares) and community respiration (R, open circles), (B) net ecosystem production (NEP), and (C) GPP : R ratio as determined from continuous O_2 measurements in Frederiksborg Slotssø from May 2003 to November 2004. R is presented as a negative number to facilitate plotting on the same graph as GPP. Negative values of NEP indicate periods where the lake consumes more oxygen in respiration than it produces in gross primary production (i.e., GPP : R $<$ 1).

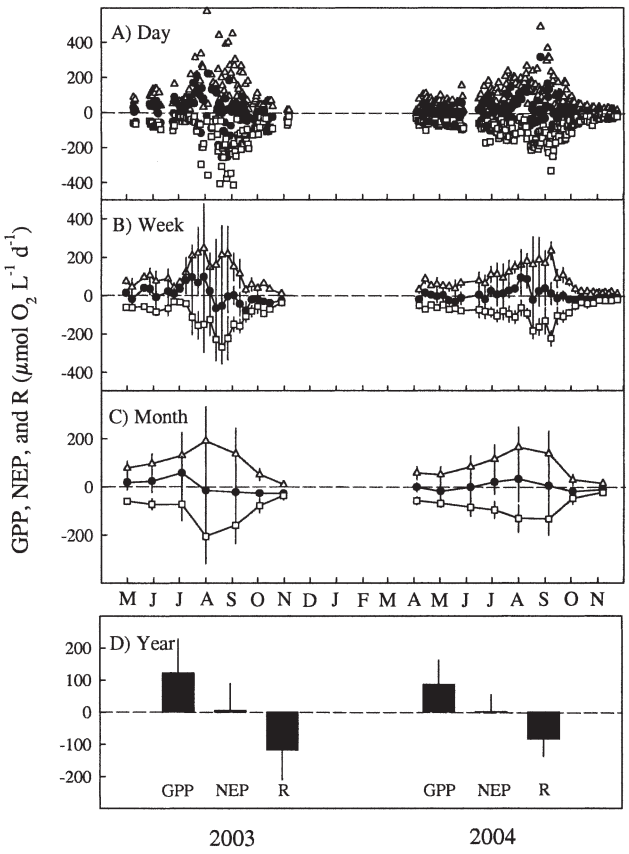

Fig. 6. Comparison of (A) daily, (B) weekly, (C) monthly, and (D) annual values of GPP (open triangles), NEP (closed circles), and R (open squares). Error bars are ±1 SD.

iksborg Slotssø because increasing net autotrophy is proposed to occur in nutrient-rich productive aquatic ecosystems (del Giorgio and Peters 1994; Schindler et al. 1997; Pace and Cole 2000).

Estimates of daily R and GPP were based on the classical assumption that R_{night} and R_{light} are equal. Different studies, however, suggest that R_{light} tends to be equal to or larger than R_{night} as a result of involvement of several biochemical pathways in addition to mitochondrial dark respiration (e.g., Bender et al. 1987; Grande et al. 1991). Because no method is available to measure R_{light} on a routine and continuous basis, we have to accept this uncertainty in the estimates of R and GPP. Moreover, if R_{light} exceeds R_{night}, the magnitude of GPP and R would be increased by equal amounts, the influence on the GPP : R-ratio would remain small (Cole et al. 2000), and there would be no change in NEP.

In agreement with previous studies on lake metabolism (Quay et al. 1995; Duarte and Agusti 1998; Cole et al. 2000), we found a positive relationship between community respiration and gross primary production. In our study, GPP exceeded R at gross primary production rates above 90 μmol O_2 L^{-1} d^{-1}, which compares well with Cole et al. (2000), who found that lakes on an average were net autotrophic at GPP above 80 μmol O_2 L^{-1} d^{-1}. In accordance with previous findings for eutrophic lakes (Cole et al. 2000), GPP and R increased with increasing algal biomass. Variations in the GPP : R ratio were,

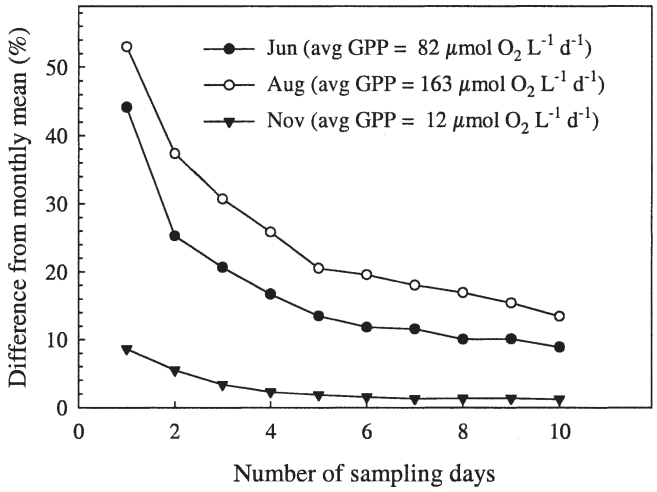

Fig. 7. Difference between monthly means of GPP in June, August, and November 2004 and the values obtained by averaging over 1 to 10 sampling days.

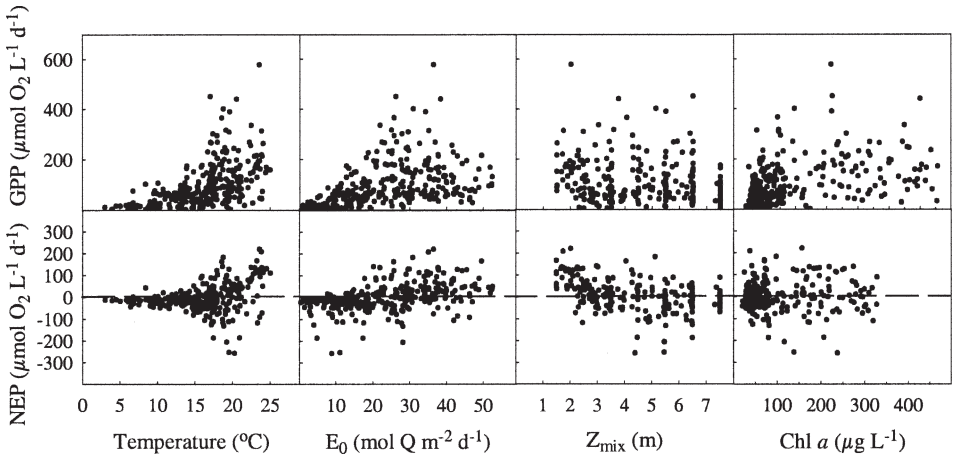

Fig. 8. Relationships between GPP, NEP, and daily values of temperature, surface irradiance (E_0), mixing depth (Z_{mix}), and Chl *a*.

however, not related to variations in algal biomass, but strongly related to changes in mixing depth, light, and temperature conditions. Input of terrestrial organic material from land can significantly increase bacterial respiration and reduce GPP : R values in aquatic ecosystems, but this input to Frederiksborg Slotssø is very low (<2% of GPP; Andersen and Jacobsen 1979), so the oxygen mass balance predominantly reflects internal autotrophy and heterotrophy based on production and decomposition of autochthonous matter.

During summer stratification, about 25% of the water volume and 20% of the bottom area are located in the hypolimnion without immediate contact to surface waters. Because no light is available in the deeper strata, respiration results in depletion of oxygen and accumulation of reduced substances (i.e., Fe^{2+}, S^{2-}, CH_4; Andersen and Jacobsen 1979). These conditions will not affect lake gross photosynthesis but may temporarily lead to underestimation of lake respiration and overestimation of GPP : R-ratios. Day-to-day variations in mixing depth (Fig. 3A) do, however, result in frequent injections of oxygen-poor bottom water into the epilimnion. Such inputs are indicated by a strong negative relationship between NEP and mixing depth (Table 2). Changes in mean light availability with mixing depth will, however, have the same effect. We used data on lake bathymetry and daily values of mixing depth to calculate the day-to-day exchange of water ($m^3\ d^{-1}$) between epi- and hypolimnion. From frequent oxygen profiles (every second week, $n = 51$) we found that the hypolimnic oxygen concentration just below the mixing depth, on average was 20% of the oxygen concentration in the epilimnic water. When we combined these data, we found that input of hypolimnic water through lowering of the mixing depth could explain 55 ± 6% (average ± SE) of the changes in measured daily respiration rates. This input, however, only occurred during 20% of the summer period, implying that in the remaining 80% of the data set, changes in mixing depth affected GPP, NEP, and R through alterations in light availability.

Injections of hypolimnic water should not affect our annual estimates of NEP and GPP : R. According to Andersen and Jacobsen (1979), only about 10–15% of lake respiration is occurring without contact with the mixed surface waters during summer stratification such that GPP : R-ratios are overestimated by approximately the same percentage. Subsequently, when stratification vanishes in the autumn, the hypolimnion becomes reoxygenated and the accumulated reduced substances reoxidized resulting in increased R and reduced GPP : R values for a while. Thus, the calculated GPP : R values slightly overestimate entire lake metabolism in summer and underestimate them in fall, but on an annual basis the integrated values are correct. Even if we correct for a mean overestimation of GPP : R values during summer of 12.5%, the actual values would still remain significantly above 1.0 (1.41 in 2003 and 1.06 in 2004).

Regulation of ecosystem metabolism—Gross primary production of lake phytoplankton is regulated by environmental and biological factors determining the biomass and physiological state of algae on daily to monthly scales as well as by factors determining the daily production rates for a certain biomass and species composition. Daily GPP values were strongly related to temperature and chlorophyll biomass with temperature being the strongest single predictor when the entire data set was analyzed (Table 3). Absence of temperature control in the seasonal data sets (Table 3), however, demonstrates that the temperature dependence seen in Fig. 8 is not caused primarily by direct effects of temperature on metabolic rates. The apparent temperature effect is due to the dampened seasonal course of temperature being coupled to available irradiance and algal biomass (Table 2). High summer temperatures are furthermore associated with formation of blue-green algal blooms during periods of low mixing depth and consequently high rates of GPP. The relatively weak coupling of GPP and NEP to environmental variables during the highly productive, nutrient-poor and stratified summer period,

Table 3. Stepwise multiple linear regression models of GPP, R, and NEP (μmol O_2 L^{-1} d^{-1}) and GPP : R as a function of water temperature (at 0.5 m depth), daily surface irradiance (mol photons m^{-2} d^{-1}), Chl *a* (μg L^{-1}), wind speed at 10 m above surface (m s^{-1}) and mixing depth (m). Only parameters that fulfilled the required significance level of $p < 0.05$ are shown. To evaluate the importance of seasonal contrasts on the regulatory importance of the different variables, the analysis was performed on seasonal data sets and all available data.

Dependent variable	Season	Parameter	*n*	Overall r^2	Partial r^2	Coefficient	*p*
GPP	Spring	E_0	58	0.67	0.46	2.08	<0.0001
		Wind			0.17	1.41	<0.0001
		Temperature			0.04	0.82	0.0120
	Summer	Chl *a*	133	0.29	0.14	0.35	<0.0001
		Wind			0.07	−11.21	0.0012
		E_0			0.06	1.84	0.0019
		Temperature			0.02	6.16	0.0465
	Fall	Z_{mix}	112	0.67	0.49	−43.81	<0.0001
		E_0			0.12	2.96	<0.0001
		Chl *a*			0.03	0.30	0.0062
		Wind			0.03	−7.65	0.0080
	All	Temperature	304	0.44	0.29	4.44	<0.0001
		Wind			0.06	−10.71	<0.0001
		Chl *a*			0.05	0.38	<0.0001
		E_0			0.04	1.70	<0.0001
R	Spring	Chl *a*	58	0.21	0.21	0.83	0.0003
	Summer	Chl *a*	133	0.35	0.25	0.45	<0.0001
		Z_{mix}			0.08	13.72	<0.0001
		E_0			0.02	−1.09	0.0400
	Fall	Temperature	112	0.57	0.54	10.76	<0.0001
		Z_{mix}			0.03	−18.09	0.0053
	All	Chl *a*	304	0.32	0.25	0.27	<0.0001
		Z_{mix}			0.04	11.67	<0.0001
		Temperature			0.03	7.66	0.0007
NEP	Spring	E_0	58	0.68	0.42	2.00	<0.0001
		Wind			0.16	−6.76	<0.0001
		Temperature			0.07	−4.42	0.0019
		Z_{mix}			0.03	−4.89	0.0458
	Summer	Z_{mix}	133	0.43	0.24	−20.89	<0.0001
		E_0			0.13	2.91	<0.0001
		Wind			0.06	−10.20	0.0002
	Fall	Z_{mix}	112	0.39	0.13	−28.72	<0.0001
		Temperature			0.08	−10.14	0.0006
		Chl *a*			0.07	0.28	0.0011
		Wind			0.06	−4.93	0.0213
		E_0			0.05	2.21	0.0401
	All	E_0	304	0.30	0.20	1.68	<0.0001
		Wind			0.07	−7.46	<0.0001
		Z_{mix}			0.03	−6.31	0.0013

suggests that exchange of organic and inorganic material across the thermocline may be an important driver of metabolic rates in the epilimnion. Future studies of daily variations in metabolism of stratified lakes should pay further attention to this source of variation.

Over longer timescales of weeks and months the biomass and physiological state of phytoplankton are markedly influenced by inorganic nutrient availability, mixing regime and food web structure in addition to the impact of irradiance and temperature (Harris 1986). In Frederiksborg Slotssø, inorganic N, P, and Si all decreased significantly during periods of high algal biomass and production in spring and summer. The marked depletion of DIC, high pH, and low CO_2 concentrations between 1 and 5 μmol L^{-1} during the bloom of blue-greens can also constrain photosynthetic production. Half-saturation constants for uptake of key nutrients have frequently been used to assess the potential for kinetic nutrient limitation of primary productivity (e.g., Petersen et al. 1997). Assuming that constants obtained for marine phytoplankton can be applied for freshwaters we found that the phytoplankton community periodically experienced N and P limited growth during summer and Si limitation in spring. The possibility of N and P stimulation of metabolic rates during periods of potential limitation was examined by applying a time lag of 7 d between weekly estimates of N and P and weekly estimates of GPP. Although no significant stimulation of GPP to N or P was observed, GPP was strongly stimulated ($r = 0.77$, $p < 0.01$) by Si concentrations appearing 1 week in advance.

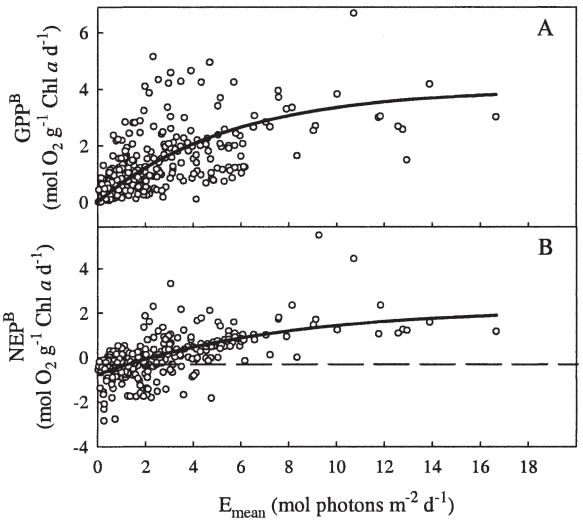

Fig. 9. Relationship between the daily mean available light level (E_{mean}) in the mixed surface layer and chlorophyll-normalized values of (A) gross primary production (GPP^B) and (B) net ecosystem production (NEP^B). Photosynthetic parameters were determined by a nonlinear regression fit of photosynthesis (P) normalized to Chl *a* (P^B) as a function of irradiance (E_{mean}) according to a saturating exponential model (Webb et al. 1974), modified for NEP^B by including an offset (c for NEP^B at E_{mean} = 0): $NEP^B = NEP^B_{max}(1 - \exp(-\alpha^B E_{mean}/NEP^B_{max})) + c$, where α^B is the initial slope of the curve and NEP^B_{max} is the light-saturated net ecosystem photosynthetic rate. The offset (c) was incorporated to avoid the bias in the estimate of α^B, which occurs when the curve is forced through the origin (Markager et al. 1999). The saturation irradiance (E_k) was calculated as NEP^B_{max}/α^B. The light compensation level (E_C) was determined as $E_C = NEP^B_{max} \log(1 + c/NEP^B_{max})/-\alpha^B$.

Phytoplankton biomass is influenced by mixing depth both directly because deeper mixing reduces mean available irradiance (E_{mean}) for the algae and, thereby, their growth capacity and indirectly because deeper mixing can inject new nutrients into the surface layers and stimulate photosynthesis and growth after a few days' delay. Daily GPP, NEP, and GPP : R in Frederiksborg Slotssø were significantly negatively related to mixing depth for data covering the entire year and they were significantly positively related to E_{mean}. The abrupt formation and collapse of summer blooms of algae followed the shifts in mixing depth and mean irradiance in the mixed surface layer, were accompanied by substantial changes from positive GPP : R-ratios during summer stratification of low mixing depth to negative GPP : R values during deep mixing in fall and early spring.

Formation and collapse of summer blooms of phytoplankton are also influenced by temporal changes in zooplankton grazing (Markager et al. 1994). Establishment of carbon budgets in Frederiksborg Slotssø based on frequent sampling for a 9-week period suggested that biological succession was determined by the balance between areal primary production and community grazing (Markager et al. 1994). A clear-water phase of comparatively low phytoplankton biomass was established by a combination of low surface irradiance, low primary production and high community grazing, whereas the bloom of blue-greens was established during a period of high irradiance and low community grazing probably coupled to intense fish predation on daphnids and dominance of inedible algae.

Regulation of metabolic rates normalized to algal biomass—In this steep-sided lake without a significant productivity from benthic macrophytes, daily gross production normalized to phytoplankton biomass (GPP^B) can serve as an index of the relative growth potential of the algae. This property was highly significantly related to E_{mean} following a hyperbolic saturation curve similar to that commonly used to describe photosynthetic performance in batch cultures of algae exposed to a gradient of fixed light levels. It is noteworthy that this relationship was remarkably strong considering the substantial underlying variations in temperature, species composition, nutritional state and irradiance between the days that were not accounted for. Moreover, the calculation of E_{mean} assumes that the phytoplankton community is circulated throughout the mixed zone, and this is hardly the case on very calm days and for positively buoyant blue-greens, which may consequently experience a more suitable light climate. Also, net ecosystem metabolism normalized to algal biomass (NEP^B) was significantly positively related to E_{mean} such that rates, on an average, were positive and indicated a scope for net growth of the total plankton biomass above 2.3 mol photons m^{-2} d^{-1} confirming the strong influence of irradiance for the biomass dynamics of the plankton community. This irradiance threshold to attain positive values of NEP^B was surpassed during 54% of the days during the summer periods in 2003 and 2004.

Effect of timescale—The relatively high day-to-day variability in metabolic rates reflects the dynamic behavior of the lake ecosystem in response to changes in incident irradiance and available irradiance in the mixed surface layers. In contrast, algal biomass is much less variable as it integrates growth and loss processes over longer periods. To attain accurate estimates of mean weekly and monthly values, it is therefore necessary to perform very frequent measurements. For example, during the late summer maximum of blue-greens in August of 2003, GPP varied between days from 14 to 578 μmol O_2 L^{-1} d^{-1} (CV 76%), R varied from 19 to 407 μmol O_2 L^{-1} d^{-1} (CV 55%) and NEP varied from -257 to 220 μmol O_2 L^{-1} d^{-1} (CV 56%). A few discrete measurements therefore cannot provide the confident picture of lake metabolism that averages of many measurements can. Despite the fact that the lake is highly net autotrophic during the period studied, some few measurements can give the false impression of net heterotrophy. The calculated coefficients of variation showed that GPP values are much more variable than R values that are anticipated because of the direct influence of the variable daily irradiance on GPP.

Variations in areal rates should in theory be smaller than volumetric rates because we are dealing with a system where most of the light attenuation is attributable to plankton

pigments (Wofsy 1983). However, having calculated vertical integrals of GPP by multiplying the volumetric rates with the mixing depth, we found that seasonal patterns and day-to-day variability of areal rates were similar to the volumetric rates. Thus, the CV for weekly, monthly, and yearly averages of GPP_{areal} was 55, 63, and 88%, compared with 55, 61, and 87% for the volumetric rates.

Frequent daily measurements of metabolic rates permitted calculation of average weekly and monthly values. Weekly averages still maintained the characteristic seasonal peaks and troughs also observed for algal biomass, whereas monthly means smoothed the data to such an extent that distinct blooms were lost, and only a broad late-summer maximum persisted. It is noteworthy that the frequent measurements also permitted calculations of accurate summer and annual means revealing slightly higher GPP values in 2003 than 2004 (Fig. 6). Mean areal rates of GPP (mol O_2 m^{-2} d^{-1}) also remained higher for 2003 (0.54 $\pm$ 0.05 mol O_2 m^{-2} d^{-1} $\pm$ SE) than 2004 (0.38 $\pm$ 0.02 mol O_2 m^{-2} d^{-1} $\pm$ SE). The main reason is probably the higher mean available irradiance in the mixed surface layer (E_{mean}) during the growth season in 2003 (5 mol photons m^{-2} d^{-1}) than in 2004 (3.2 mol photons m^{-2} d^{-1}). The possible scenario, as previously proposed by Markager et al. (1994), is that low available irradiance and the associated low GPP and GPP : R values will allow zooplankton to play a stronger controlling role as grazers on the phytoplankton biomass leading to its distinct decline. When the seasonal course of phytoplankton and zooplankton biomasses are determined by a delicate balance between growth and loss processes, and when the positive balance increases markedly with standing biomass because high biomasses can produce more and lose less algal cells, relatively small changes in environmental variables can push the biomass across boundaries where either blooms or collapses occur. To reach an understanding of such phenomena, continuous measurements such as those presented here are essential.

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