

Lake metabolism scales with lake morphometry and catchment conditions

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Abstract We used a comparative data set for 25 lakes in Denmark sampled during summer to explore the influence of lake morphometry, catchment conditions, light availability and nutrient input on lake metabolism. We found that (1) gross primary production (GPP) and community respiration (R) decline with lake area, water depth and drainage ratio, and increase with algal biomass (Chl), dissolved organic carbon (DOC) and total phosphorus (TP); (2) all lakes, especially small with less incident light, and forest lakes with high DOC, have negative net ecosystem production ($NEP < 0$); (3) daily variability of GPP decreases with lake area and water depth as a consequence of lower input of nutrients and organic matter per unit water volume; (4) the influence of benthic processes on free water metabolic measures declines with increasing lake size; and (5) with increasing lake size, lake metabolism decreases significantly per unit water volume, while depth integrated areal rates remain more constant due to a combination of increased light and nutrient limitation. Overall, these meta-parameters have as many significant but usually weaker relationships to whole-lake and benthic metabolism as have TP, Chl and DOC that are directly linked to photosynthesis and respiration. Combining water depth and Chl to predict GPP, and water depth and DOC to predict R, lead to stronger multiple regression models accounting for 57–63% of the variability of metabolism

among the 25 lakes. It is therefore important to consider differences in lake morphometry and catchment conditions when comparing metabolic responses of lakes to human impacts.

Keywords Lake metabolism · Lake morphometry · Catchment conditions · Intrinsic drivers · Temporal variability

Introduction

Research on lake metabolism has shown that gross primary production (GPP), respiration (R) and net ecosystem production ($NEP = GPP - R$) vary considerably among lakes and over time within lakes (Cole et al. 2000; Hanson et al. 2006; Staehr and Sand-Jensen 2007; Staehr et al. 2010a). Many lakes have a negative NEP and most release CO_2 to the atmosphere. This is due to the considerable supply and substantial degradation of allochthonous organic material from the surrounding landscape (Sand-Jensen and Staehr 2007, 2009). While day-to-day differences in metabolism within a lake are primarily driven by changes in light, temperature and vertical mixing (Hanson et al. 2006; Staehr and Sand-Jensen 2007), long-term differences in metabolism between lakes are strongly related to changes in concentrations of total phosphorus (TP), phytoplankton chlorophyll (Chl) and dissolved organic carbon (DOC) (Sand-Jensen and Staehr 2007, 2009). Thus, autotrophic lakes ($NEP > 0$) typically have high TP, high Chl and low DOC concentrations, whereas the most heterotrophic lakes have low TP, low Chl and high DOC (Hanson et al. 2003; Sand-Jensen and Staehr 2007).

Lake morphometry (surface area and depth), catchment properties (geology, size and land use) and hydrology have

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a strong influence on lake temperature, physical mixing, nutrient concentrations, DOC, Chl and transparency (Fee et al. 1996; Hanson et al. 2007; Nöges 2009), suggesting that these conditions operate as meta-parameters with an indirect but potentially strong effect on lake metabolism. Implicit scaling of lake productivity to lake size has been considered for decades (Thienemann 1927; Brylinsky and Mann 1973; Fee et al. 1992), and location in forests or open landscapes is also known to affect metabolism (Tranvik 1992; del Giorgio and Peters 1994; Sand-Jensen and Staehr 2007, 2009). Thus, lake area is statistically positively related to wind exposure, water depth and mixing depth and inversely related to external input of nutrients and DOC per water volume and surface area (e.g., Brylinsky and Mann 1973; Duarte and Kalff 1989; Fee et al. 1996). Drainage ratio (catchment area:lake area) is positively related to external input of nutrients, CO₂ and DOC (Gergel et al. 1999). Forest cover is negatively correlated with nutrient input and incoming irradiance for small lakes and positively correlated with DOC input and light attenuation by coloured DOC (Xenopoulos et al. 2003; Sand-Jensen and Staehr 2007).

In contrast to the substantial literature on the importance of meta-parameters for lake chemistry and physics, there are few comparative measurements of whole-lake metabolism, for a sufficiently large number of lakes, to evaluate the importance of lake size and catchment conditions on whole-lake metabolism and atmospheric CO₂ exchange. This study investigates the effect of these meta-parameters on GPP, R and NEP, and compares their role with that of traditional direct drivers of metabolism (i.e., Chl, DOC, light and temperature). Our general expectation is that meta-parameters are significant though probably not as strong predictors of GPP, R and NEP as the intrinsic variables directly involved in metabolic processes. If so, more general predictive models can be derived and new understanding of control mechanisms can be obtained.

Our first specific prediction is that both volumetric GPP and R should decline with increasing lake area, water depth and drainage ratio, as the concentrations and input of nutrients and DOC decrease (Nöges 2009). Although light availability decreases with increasing depth of the photic zone, light availability, is, however, expected to be similar across lake sizes as lower inputs of light absorbing material and greater mixing depth in larger lakes should cause mean light availability to remain similar among lakes of different sizes. Areal rates of GPP integrated over the entire water column is therefore expected to vary little with lake size, and the influence of lake size for GPP expected to be higher for volume specific rates.

Our second specific prediction is that small lakes should have higher DOC input and concentrations and be more net

heterotrophic (NEP < 0) than large lakes and that forest lakes should be more net heterotrophic than lakes in open landscapes. Small lakes have a greater contact and possibility of exchange of organic material with the terrestrial landscape along its periphery relative to lake surface area than large lakes. Forest lakes have a direct transfer of litter from the surrounding tree vegetation, receive less light for photosynthesis on the lake surface and have higher DOC concentrations in the water column competing with photosynthetic pigments for available photons causing mean light availability to remain low despite of a shallow mixed depth (Staehr et al. 2010a). Conversely, reduced input of DOC in larger lakes should favour positive NEP as mean light availability for primary production is the same but less allochthonous material is supplied for bacterial oxygen consumption. A final mechanism may restrict benthic photosynthesis relative to respiration in small forest lakes, namely the typical organic-rich sediments of flocculated humic material of low mass density that is physically instable for microalgae and unfavourable for growth of rooted plants (Barko and Smart 1986; Sand-Jensen et al. 2005).

Our third specific prediction is that the contribution of benthic processes to whole-lake metabolism declines with increasing water depth. Because light penetration to sediments decreases with water depth, the benthic primary production should be more constrained by water depth than respiration and this should be particularly so in forest lakes with high DOC concentrations and poor light conditions. To the extent that lake depth and lake area are correlated, the role of benthic processes should also decline with increasing lake area, while surrounding forest vegetation may stimulate benthic R but impede GPP and NEP.

Our fourth specific prediction is that the day-to-day variability of lake metabolism should decline with increasing lake area and depth. Measurements of whole-lake metabolism were performed over 1 week in each lake for subsequent comparison among all 25 lakes. This duration permits reliable calculations of mean daily metabolism and mean values for other physical, chemical and biological properties (Hanson et al. 2003; Staehr and Sand-Jensen 2007). Moreover, 1 week measurements permit calculation of daily variability of metabolic parameters and their relationship to meta-parameters and within-lake parameters. With increasing lake area and water depth, temporal variations in the magnitude of physical mixing affecting different pelagic populations are likely to decline. Reduced external input of nutrients and DOC per unit water volume with increasing lake size should also reduce the carrying capacity for phytoplankton, zooplankton, bacteria and fish per unit volume and, thereby, dampen population changes and blooms.

Materials and methods

Study sites

We studied lake metabolism in relation to physical, chemical and biological characteristics for about 1 week (6–8 days) in 25 medium to high alkaline lakes during May and June 2007. Systems ranged from ponds (0.1 ha) to mid-sized (1,729 ha) lakes, and were all located in calcareous moraines in Denmark (Table 1). Lakes were sampled in a random order to avoid bias from changing meteorological conditions during the study. Throughout the study, meteorological conditions were measured from a buoy placed on Lake Slotssø. Daily average wind speed ($0.3\text{--}5.4\text{ m s}^{-1}$, min–max) and solar irradiance ($5\text{--}55\text{ mol photons m}^{-2}\text{ day}^{-1}$) showed large daily variability, but did not change significantly during the course of the study. Lakes were chosen to cover large ranges in lake size, forest cover, TP, Chl and DOC concentrations. Lake area, catchment area, %forest cover in the catchment and drainage ratio (catchment area:lake area) were obtained for each lake using the digital Areal Information System (Nielsen et al. 2000). To evaluate effects of forest cover on local wind and light conditions, we also determined the proportion of forest in the 200 m wide riparian zone around the lakes from aerial photographs.

Limnological variables

Triplicate water samples were collected once from each lake as a depth integrated sample from the upper mixed layer at the center between 10 and 12 o'clock. Samples were analyzed for chlorophyll a, DOC, nutrients, alkalinity and pH. Samples for Chl and phaeopigments were filtered through Advantec® GC-50 filters, extracted in 96% ethanol for 24 h and measured according to Jespersen and Christoffersen (1987) using a Shimadzu UV-160A spectrophotometer. Absorbance of colored dissolved organic matter (CDOM) was measured in a GF/F filtrate ($0.7\text{ }\mu\text{m}$) at 300, 340, 360 and 400 nm in a 5 cm cuvette. DOC concentrations (mg C L^{-1}) were estimated from the linear relationship to CDOM absorption at 360 nm (m^{-1}): $\text{DOC} = 0.454\text{ CDOM}_{360} + 1.9$ ($r^2 = 0.80$) found in a study of 399 water samples from Danish lakes and streams (C. Stedmon, unpubl. data). Total phosphorus (TP) was determined for unfiltered samples by persulfate digestion according to Eaton et al. (1995) and assayed according to Kragh and Sondergaard (2004). Water for determination of pH, alkalinity and CO_2 was transferred to closed, dark glass bottles to avoid CO_2 exchange with the air and prevent photosynthesis before measurement in the laboratory within 2 h. The pH was measured with Radiometer equipment (accuracy 0.01 pH unit). Acidimetric titration of alkalinity (acid neutralizing capacity, ANC), ionic strength, pH and

temperature were used to calculate concentrations of free CO_2 according to Rebsdorf (1972). The calculated CO_2 concentrations have previously been shown to be in close agreement with direct CO_2 measurements on an IRGA using a headspace equilibration technique (Sand-Jensen and Frost-Christensen 1998). Fluorescence of DOC was measured on a Varian Eclipse fluorescence spectrophotometer. An emission spectrum was measured every 2 nm between 300 and 600 nm, whilst exciting at 370 nm. The fluorescence index (FI; McKnight et al. 2001) was derived by taking the ratio of the fluorescence at 450 to that at 500 nm. This index can be used to characterize the chemical composition of DOC and indicate the relative contribution of terrestrial and aquatic organic matter. Index values typically range between 1 and 2, with terrestrial plant material resulting in low values.

Depth profiles of oxygen and temperature were recorded in situ by an YSI 600XL multisonde. The vertical light attenuation coefficient (K_D , 400–700 nm) was determined from the depth profile of photosynthetically active radiation (PAR) using a LiCor 4π sensor. K_D was calculated as the slope of a linear regression model of irradiance (E_z) versus depth (z): $\ln(E_z) = b + K_D z$.

Physics and metabolism from sonde measurements

We deployed a buoy at the centre of each lake to measure surface PAR, wind speed, water temperature and dissolved oxygen concentration (DO) for about 1 week. Three sets of this equipment were moved between lakes in a random order. Surface PAR was measured 1 m above the surface using a HOBO 2π quantum sensor. Wind speed was measured 1.2 m above the lake using a HOBO anemometer. Surface PAR and wind speed at the centre of each lake were normalized to measurements made throughout the summer in medium-sized Lake Slotssø (22 ha, 15% forest cover; Table 1). Normalization was simply the ratio of the wind speed at a lake to that of Lake Slotssø. This permitted comparison among the 25 lakes despite changes in mean weekly wind velocity and surface PAR during the summer. Water temperature was measured every 10 min during buoy deployment at several water depths, using a string of Stow Away Tidbit loggers. These data permitted calculation of mixing depth (Z_{mix}) at high frequency according to an empirical curve-fitting procedure (Staehr et al. 2010a). Dissolved oxygen was measured at 0.5 m either with an Oxyguard DO sensor or a YSI 600XL multisonde. Oxygen sensors were cleaned and calibrated prior and after each application. Electrode drift was small and was corrected for assuming it is linear over time. Oxygen concentrations recorded every 10 min were used to calculate NEP for 30 min intervals, according to the guidelines presented in Staehr et al. (2010b): $\text{NEP}_{30\text{min}} = \Delta\text{O}_2 - D/Z_{\text{mix}}$, where

Table 1 Physical, optical and mean chemical characteristics for surface waters of the lakes

Lake	Area (ha)	Mean depth (m)	Forest (%)	Mixing depth (m)	K_D (m^{-1})	Chl ($mg\ m^{-3}$)	TP ($mg\ m^{-3}$)	DOC ($g\ m^{-3}$)	CO_2 (% sat)	ANC ($meq\ L^{-1}$)
Agersø	3.7	3.2	75	3.2	1.20	7.7 ± 0.2	24.5 ± 2.4	5.75 ± 0.01	280 ± 13	0.50 ± 0.01
Agertofte	0.6	0.8	74	0.7	2.82	23.9 ± 2.3	80.5 ± 2.0	22.92 ± 0.16	1,588 ± 27	1.88 ± 0.01
Badstuedam	2.8	0.7	8	1.2	2.03	7.6 ± 0.2	33.8 ± 0.6	16.28 ± 0.28	284 ± 3	3.28 ± 0.02
Bastrup Sø	32.3	3.5	11	3.3	0.96	9.9 ± 0.1	48.3 ± 1.0	6.50 ± 0.02	316 ± 14	2.52 ± 0.03
Buresø	76.1	7.0	34	4.2	0.57	4.3 ± 0.3	29.2 ± 3.2	8.45 ± 0.05	101 ± 2	2.25 ± 0.01
Bøllelose	0.5	0.8	1	1.1	2.27	28.4 ± 5.3	101.1 ± 9.3	19.51 ± 0.06	470 ± 24	2.60 ± 0.01
Esrum Sø	1,729.0	13.5	38	3.8	0.27	0.8 ± 0.0	184.2 ± 1.5	6.05 ± 0.08	67 ± 1	2.57 ± 0.01
Farumsø	120.0	6.3	26	10.3	0.65	6.3 ± 0.9	29.2 ± 0.6	9.00 ± 0.05	114 ± 4	2.95 ± 0.03
Favrholm	1.0	1.5	1	1.1	1.64	27.6 ± 1.0	54.4 ± 2.9	5.26 ± 0.01	370 ± 47	1.83 ± 0.04
Fugl sø	4.95	2.2	3	2.3	1.25	8.6 ± 0.2	56.1 ± 1.6	10.70 ± 0.03	468 ± 8	5.15 ± 0.02
Funkedam	1.6	1	85	1.3	1.10	6.1 ± 0.1	28.0 ± 3.0	6.97 ± 0.03	602 ± 6	2.04 ± 0.02
Fønstrupdam	1.1	1.6	67	0.7	1.43	8.3 ± 1.5	47.8 ± 3.1	7.67 ± 0.02	881 ± 28	1.46 ± 0.00
Grib sø	10.0	4.8	89	2.6	2.63	34.9 ± 0.6	48.4 ± 1.2	23.35 ± 0.12	ND	ND
Hampen Sø	76.0	4.3	65	6.2	0.50	4.0 ± 0.0	16.6 ± 1.6	45.64 ± 0.28	232 ± 10	0.44 ± 0.01
Hestskodam	0.5	1.5	15	1.3	2.58	31.0 ± 2.3	100.8 ± 4.1	7.62 ± 0.03	2 ± 0	1.59 ± 0.02
Karlssø	2.9	1.1	76	1.6	3.36	29.8 ± 1.9	95.0 ± 1.5	14.27 ± 0.04	1,086 ± 21	2.16 ± 0.00
Klaresø	3.4	1.6	86	1.8	5.23	402.3 ± 192.5	115.2 ± 31.0	16.84 ± 0.19	1,314 ± 291	0.22 ± 0.00
Præstevang	0.7	1.5	3	1.2	1.52	24.8 ± 10.4	40.8 ± 4.6	8.71 ± 0.22	312 ± 67	2.56 ± 0.05
Selskovvej Sø	2.3	3	27	2.1	1.05	26.1 ± 2.8	43.6 ± 0.6	7.68 ± 0.01	273 ± 14	3.56 ± 0.02
Sidseldam	0.1	0.5	91	1.4	5.66	65.3 ± 14.6	249.4 ± 30.1	3.02 ± 0.03	2,340 ± 182	1.88 ± 0.02
Sjælsø	293.0	2.8	19	2.3	0.64	6.4 ± 0.2	49.5 ± 5.1	2.58 ± 0.01	251 ± 4	2.99 ± 0.03
Slotssøen	22.1	3.5	5	4.2	1.23	18.6 ± 0.9	54.7 ± 6.9	4.40 ± 0.01	151 ± 8	2.58 ± 0.02
Sortedam	0.5	0.5	24	1.0	3.94	35.1 ± 2.2	159.1 ± 5.3	4.17 ± 0.01	142 ± 39	1.93 ± 0.03
Strødam Engsø	17.6	1	21	1.5	3.94	92.9 ± 4.8	178.4 ± 8.7	3.05 ± 0.06	394 ± 42	5.27 ± 0.10
Teglårdssø	5.3	1	57	0.8	2.14	24.0 ± 0.9	54.8 ± 1.2	5.68 ± 0.02	359 ± 40	2.15 ± 0.01

Uncertainties are SE, $n = 3$ K_D light attenuation, Chl algal biomass, TP total phosphorus, DOC dissolved organic carbon, CO_2 percent, ANC acid neutralizing capacity, ND not determined

ΔO_2 ($\text{mmol O}_2 \text{ m}^{-3} 30 \text{ min}^{-1}$) is change in oxygen concentration over 30 min, D ($\text{mmol O}_2 \text{ m}^{-2} 30 \text{ min}^{-1}$) is exchange with the atmosphere in this period and Z_{mix} (m) is mixing depth. Atmospheric exchange was calculated as $D = k(O_2 - O_{2\text{sat}})$, where O_2 is actual oxygen concentration, $O_{2\text{sat}}$ 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 Jähne 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: $k_{600} (\text{cm h}^{-1}) = 2.07 + 0.215 U^{1.7}$ according to Cole and Caraco (1998). Assuming a neutrally stable boundary layer, wind speed (U) at 10 m was calculated from our measurements at 1.2 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 $\text{GPP} - R$ (where R is in positive numbers). For ease of comparison, we present GPP values as positive and R values as negative. Volumetric metabolic rates ($\text{mmol O}_2 \text{ m}^{-3} \text{ day}^{-1}$) were turned into areal rates ($\text{mol O}_2 \text{ m}^{-2} \text{ day}^{-1}$) by multiplying with daily estimates of Z_{mix} for stratified lakes and mean water depth for fully mixed lakes.

Pelagic metabolism from bottle measurements

While calculation of whole-lake metabolism from sonde measurements are relatively common, measurements of benthic metabolism are rare because they require special sediment chambers and Scuba diving to set up and many replicates are needed because of great spatial heterogeneity. Because we wanted to make a comparative analysis among many lakes, direct sediment measurements were not an option. Instead, we evaluated the influence of benthic processes on free water measures of metabolism as the difference between measured whole-lake metabolism by oxygen sondes in open waters and simultaneous measurements of pelagic metabolism in bottle incubations.

Replicate water samples from 0.5 m depth were used to determine net photosynthesis and respiration as the rate of oxygen change in closed 10 ml bottles during incubation for 13.5–23.4 h at ambient temperature. Bottles were placed on a rotating wheel (12 rpm) in a temperature-constant incubator and illuminated by cool-white fluorescence tubes from one side. Oxygen concentrations in the samples before and after incubation were measured using

an oxygen electrode (OX500, Unisense with a picoammeter, PA2000, connected to a laptop computer). The electrode was calibrated at the incubation temperature in water at 100 and 0% air saturation. The irradiance was measured inside the incubation bottles with a minute 4π LiCor underwater light sensor. Samples were exposed to seven different irradiances ranging from 36 to 714 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ by using a set of neutral filters in front of the bottles. Samples for dark respiration measurements were wrapped in aluminum foil. From the obtained rates of net oxygen production (NP) at different irradiances (I), NP-I curves were constructed using the non-linear model of Webb et al. (1974) in SAS 9.1 (SAS Institute Inc., 1994):

$$NP = GP_{\text{max}} \times \left[1 - \exp\left(\frac{-\alpha \times E_{\text{mean}}}{GP_{\text{max}}}\right) \right] + Int$$

where NP is net and GP_{max} is maximum gross photosynthesis ($\text{mg O}_2 \text{ L}^{-1} \text{ h}^{-1}$), α is the initial slope of photosynthesis versus irradiance, Int is the intersection with the y-axis corresponding to dark respiration and E_{mean} is the mean available irradiance in the mixed zone. Daily light availability (E_{mean} ; $\text{mol photons m}^{-2} \text{ day}^{-1}$) was calculated as an average for the mixed surface zone. Using data for surface irradiance (E_0 ; $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$), mixing depth (m), and light attenuation (K_D ; m^{-1}), with a constant of 0.1 for back-scattering and surface reflection, β (Kirk 1994), E_{mean} was calculated from the equation: $E_{\text{mean}} = E_0(1 - \beta)(1 - e^{-K_D Z_{\text{mix}}})/(K_D Z_{\text{mix}})$, modified from Riley (1957).

Each NP-I curve was examined visually and obvious outliers were excluded to obtain reasonable models. NP-I models that did not saturate at high irradiance were also excluded. The calculated models yielded maximal net photosynthesis (NP_{max}), dark respiration (R), light utilization efficiency (α), light compensation point (E_C) (the irradiance of which $NP = 0$) and light saturation point ($E_K = NP_{\text{max}}/\alpha$) (the irradiance at which photosynthesis starts to saturate). Using the derived NP models and measurements of ambient irradiance, we calculated net primary production in daylight (NPP_{bottle} ; $\text{mg O}_2 \text{ m}^{-3} \text{ day}^{-1}$) by integrating hourly NP rates from sunrise to sunset as: $NPP = \text{mean NP} \times \text{h of daylight}$. Daily respiration (R_{bottle} ; $\text{O}_2 \text{ m}^{-3} \text{ day}^{-1}$) were calculated by multiplying hourly rates by 24. Daily rates of gross primary production (GPP_{bottle} ; $\text{mg O}_2 \text{ m}^{-3} \text{ day}^{-1}$) were calculated as the sum of NPP and R_{bottle} . Daily values of GPP_{bottle} and R_{bottle} were calculated for the duration of the buoy deployment and average values were finally calculated for each lake to compare with averages of sonde-based metabolic rates.

Statistical analysis

Simple relationships between metabolic rates and physical and chemical variables were evaluated using a two-tailed

Pearsons correlation analysis. All variables were log transformed to normalize distributions, ensure variance homogeneity and linearize relationships. To avoid negative NEP values in the analyses we added +1,000 to turn all NEP values positive. In our analysis, we applied $p < 0.05$ as a criteria for significant correlations. Empirical models of the variation in GPP, R and NEP as a function of lake size, forest cover were analysed by stepwise regression analysis. Only parameters which contributed significantly ($p < 0.05$) were included in the final regression models performed in SAS 9.1 (SAS Institute Inc., 1994).

Results

Lake characteristics

The 25 lakes varied substantially in surface area (0.1–1,729 ha), mean depth (0.5–13.5 m), mixing depth (0.7–10.3 m; 12 out of 25 lakes were stratified) and forest

cover in the catchment (1–91%; Table 1). Lake trophicity ranged from mesotrophy to hypereutrophy and dystrophy according to the levels of TP (17–249 mg m^{-3}), Chl (4–402 mg m^{-3}), K_D (0.5–5.7 m^{-1}) and DOC (2.6–45.6 mg L^{-1} ; Table 1). Lakes were medium to high alkaline (ANC; $2.3 \pm 0.1 \text{ mEq L}^{-1}$ mean \pm SE) and usually supersaturated (22 lakes) with CO_2 (Table 1). With increasing lake surface area, lakes became deeper, had deeper mixing depth (Table 2), were more wind exposed and received more incident light (Fig. 1; Table 2). Forest cover was not related to lake surface area and mean water depth (Table 2), but wind exposure and surface irradiance declined significantly with forest cover (Fig. 1b, d; Table 2).

With increasing surface area, deeper water and lower drainage ratio, lakes contained less phosphorus, were more transparent and had significantly less phytoplankton (Chl), while none of these variables were significantly correlated to forest cover (Fig. 2; Table 2). As anticipated, the vertical attenuation coefficient K_D was closely positively

Table 2 Pearsons correlation coefficients among lake morphometry and catchment properties (lake area, mean water depth, drainage ratio (catchment area to lake area), %forest in lake catchment, and surrounding the lake (used only for comparison with Z_{mix} , %light and %wind), optical conditions (light attenuation coefficient (K_D), mean available irradiance (E_{mean})), meteorological conditions (% light and

% wind relative to surface PAR and wind measured at Castle lake), mixing depth (Z_{mix}), algal biomass (Chl), dissolved organic carbon (DOC), fluorescence index (FI), chemical variables (total phosphorus (TP), % CO_2 saturation) and metabolic rates (volumetric (vol) and areal) of GPP, R and NEP, including influence of benthic metabolism on whole lake measures (sonde-bottle)

	Area	Depth	Drainage ratio	%Forest	Z_{mix}	Chl	DOC	TP
GPP _{vol}	-0.54	-0.65	0.53	-0.13	-0.62	0.69	0.60	0.70
R _{vol}	-0.64	-0.70	0.58	0.04	-0.67	0.68	0.72	0.75
NEP _{vol}	0.44	0.38	-0.32	-0.42	0.36	-0.32	-0.61	-0.46
GPP _{areal}	0.17	0.21	0.14	-0.02	0.32	0.31	0.13	0.15
R _{areal}	0.09	0.18	0.11	0.12	0.29	0.30	0.24	0.13
NEP _{areal}	0.15	0.01	0.02	-0.33	-0.11	-0.22	-0.43	-0.13
GPP _{sonde-bottle}	-0.42	-0.50	0.39	-0.08	-0.45	0.59	0.49	0.52
R _{sonde-bottle}	-0.54	-0.55	0.50	0.14	-0.57	0.56	0.73	0.55
NEP _{sonde-bottle}	0.43	0.37	-0.40	-0.36	0.43	-0.30	-0.68	-0.36
CO ₂ sat	-0.50	-0.40	0.65	0.40	-0.30	0.30	0.49	0.17
FI	0.54	0.42	-0.41	-0.32	0.35	-0.59	-0.82	-0.31
K_D	-0.67	-0.71	0.60	0.16	-0.61	0.88	0.87	0.87
E_{mean}	0.27	0.16	-0.27	-0.17	-0.16	-0.57	-0.54	-0.41
%Light	0.57	0.40	-0.33	-0.41	0.42	-0.27	-0.52	-0.32
%Wind	0.80	0.67	-0.47	-0.51	0.76	-0.41	-0.65	-0.30
Area	–	0.84	-0.68	0.09	0.74	-0.57	-0.59	-0.45
Depth	–	–	-0.78	0.11	0.83	-0.56	-0.58	-0.61
Drainage ratio	–	–	–	-0.12	-0.56	0.52	0.57	-0.20
%Forest	–	–	–	–	0.01	0.04	0.41	0.01
Z_{mix}	–	–	–	–	–	-0.46	-0.53	-0.52
Chl	–	–	–	–	–	–	0.77	0.78
DOC	–	–	–	–	–	–	–	0.65

Analysis was performed on log-transformed data. Bold indicates significant correlations ($p < 0.05$). Correlations above 0.49 are significant at $p < 0.01$; $n = 25$

Fig. 1 Relationships of relative wind and relative light exposure to lake area and percent forest cover in the riparian zone. Percent wind and percent light were determined as the weekly average wind speed and irradiance at the center of each lake relative to that of a mid-sized lake (Slotssøen; Table 1). Errors are \pm SE

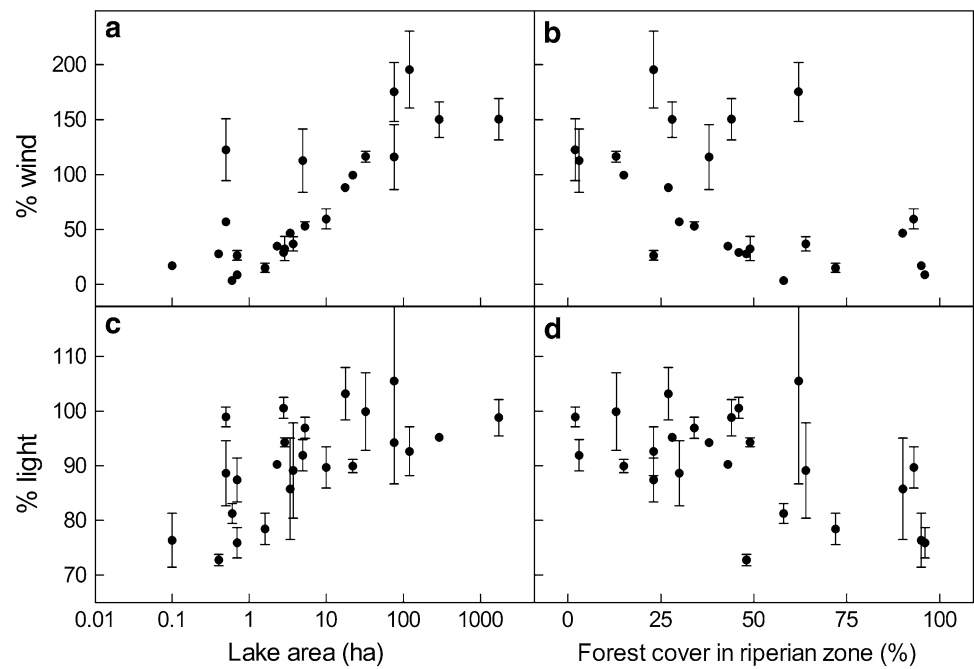


Fig. 2 Relationships of total phosphorus (TP), chlorophyll (Chl), and light attenuation (K_D) with lake area and percent forest cover in the catchment. Errors are \pm SE. TP value marked with a circle represents Esum sø and was not included in the statistical analysis as this lake is historically known to be nitrogen limited. Only one K_D value was determined for each lake

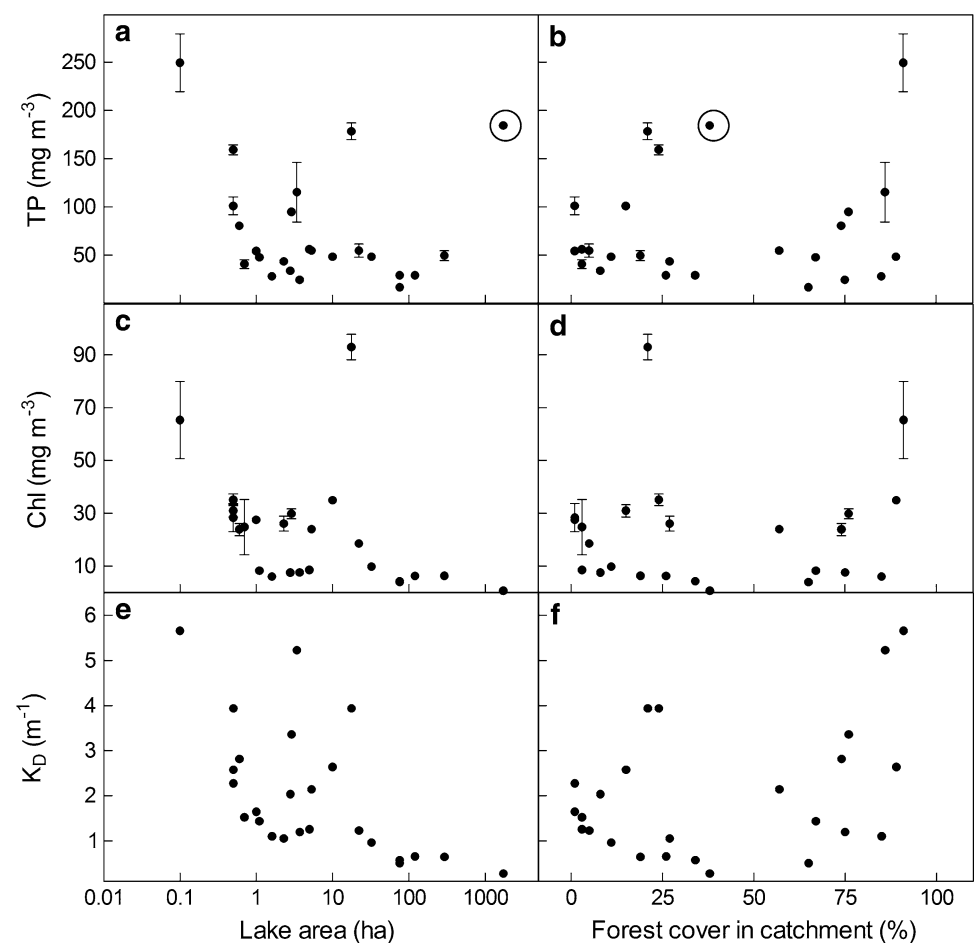
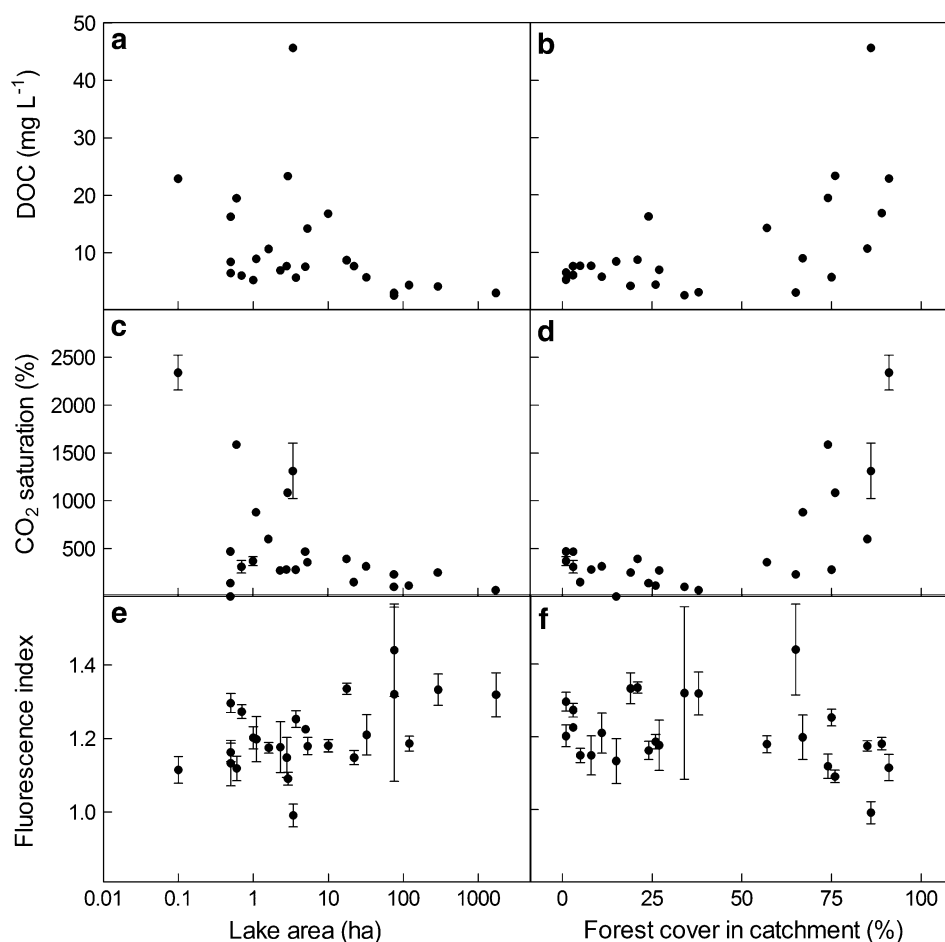


Fig. 3 Relationships of dissolved organic carbon (DOC), CO₂ saturation, and fluorescence index with lake area and percent forest cover in the catchment. Errors are \pm SE. Errors for DOC are smaller than the used symbol



correlated with both Chl and DOC (Table 2), causing the mean irradiance available for photosynthesis in the mixed surface layer to decline significantly as lakes became either brown-colored or rich in nutrients and phytoplankton. Mean light availability was, as expected, not related to lake area or depth (Table 2) because larger and deeper lakes are clearer but mix deeper. DOC and CO₂ saturation decreased with higher lake area and water depth and increased with forest cover and drainage ratio (Fig. 3a–d; Table 2). The fluorescence index was lowest for small and forested lakes and increased significantly with lake area (Fig. 3e, f), mean depth and drainage ratio, but declined with forest cover and DOC (Table 2), supporting the expectation that high DOC in small lakes and lakes with high forest cover originates from terrestrial material, whereas autochthonous production of DOC prevails in larger lakes in open landscapes.

Lake metabolism

Volumetric rates of GPP and R declined more than fivefold with increasing lake area, while correlations with forest cover were not significant (Fig. 4a–d; Table 2). NEP was negative in 14 lakes, positive in only two lakes and close to

zero in the remaining 8 lakes (Fig. 4e, f). For one lake, sonde data were lost, and metabolic rates not calculated. NEP correlated with CO₂ saturation ($r = -0.48$, $p = 0.02$), and NEP became significantly more negative as lake area declined and forest cover and DOC increased (Table 2). Consequently, the most negative NEP rates were observed in DOC and CO₂ rich lakes smaller than 1 ha located in catchments dominated (>60%) by forest.

Volumetric rates of GPP and R were significantly correlated with each other ($r = 0.91$, $p = 0.006$) and positively correlated with TP, Chl and DOC (Table 2). R increased significantly more than GPP with higher DOC concentrations, causing NEP to become significantly more negative and CO₂ super saturation to increase (Table 2). Correlations of GPP, R and NEP with lake surface area, water depth, drainage ratio and forest cover (only NEP) were often not as strong as correlations with intrinsic variables (e.g., TP, Chl and DOC) closely coupled to metabolic processes (Table 2).

In contrast to the highly significant relationships of volumetric rates (mmol O₂ m⁻³ day⁻¹) of GPP, R and NEP to lake size and catchment properties (only NEP), areal rates of metabolism (mmol O₂ m⁻² day⁻¹) were less

Fig. 4 Relationships of gross primary production (GPP), respiration (R) and net ecosystem production (NEP) with lake area and percent forest cover in the catchment. Errors are \pm SE

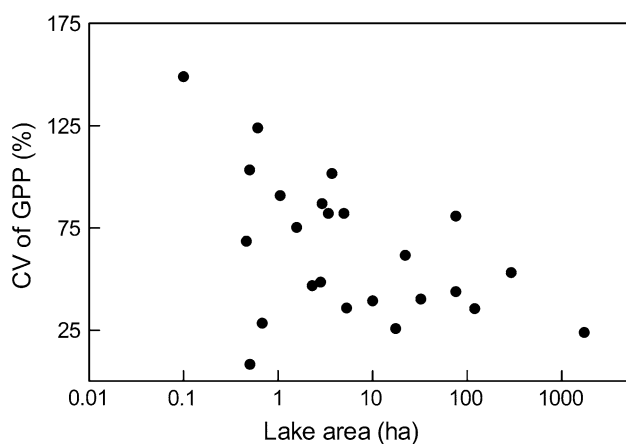
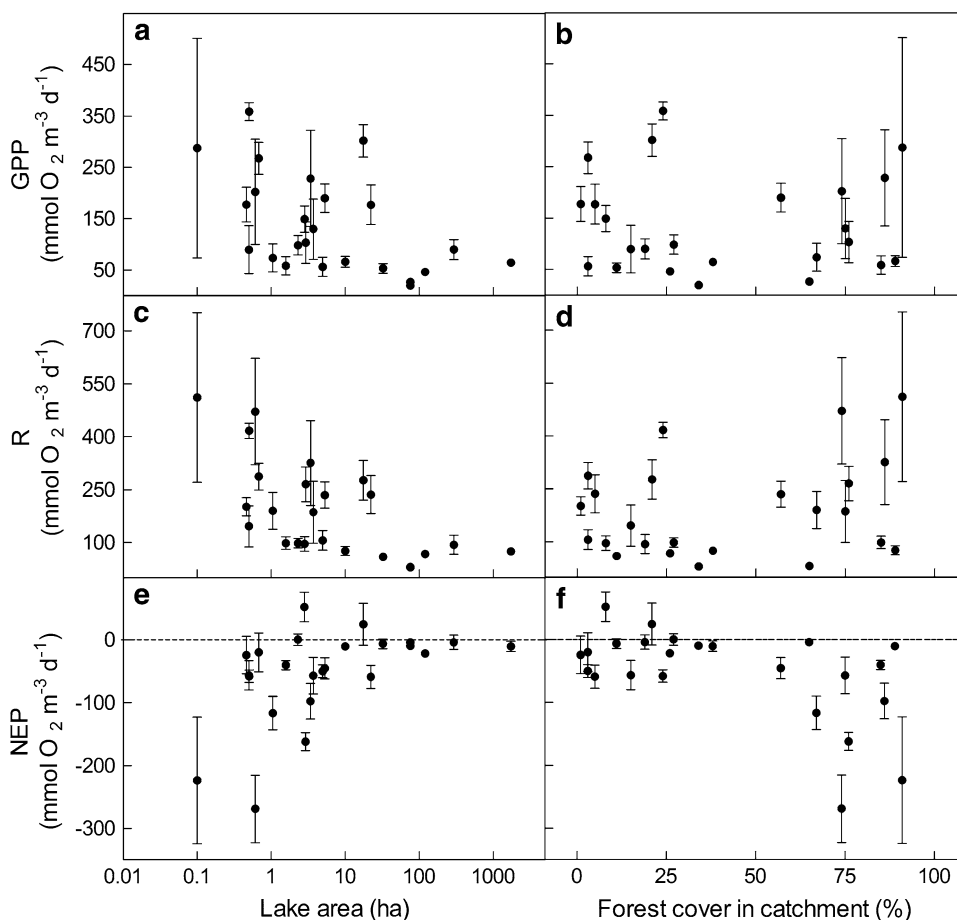


Fig. 5 Coefficient of variation (SD/mean) of GPP in relation to lake area

strongly related to these meta-parameters and showed no relationship with either DOC, TP or Chl (Table 2).

Day-to-day variability of GPP, R and NEP, can be described by the standard deviation (SD) of metabolism over the period of measurement and by the coefficient of variation being the standard deviation normalized to the mean ($CV = SD/X_{\text{mean}}$). Both in absolute (SD; $r = -0.46$,

$p = 0.02$) and relative terms (CV; $r = -0.44$, $p = 0.03$; Fig. 5), the daily variability of GPP declined with lake area as we had anticipated and it was highest in small lakes receiving high inputs of exogenous nutrients and DOC.

The influence of benthic processes on rates of whole-lake metabolism was evaluated by subtracting measured pelagic rates (bottle incubations) from sonde based rates using the diel open water technique. According to the sonde-bottle estimates of GPP and R, the influence of benthic processes declined significantly with increasing lake area, water depth and drainage ratio (only R, but almost GPP), but showed no significant relationship to forest cover (Fig. 6a, b; Table 2). Since sonde estimates of whole-lake NEP were generally more negative than bottle estimates of pelagic NEP, the $NEP_{\text{sonde-bottle}}$ estimates were mostly negative (Fig. 6c; 19 lakes in total). As lake area and water depth increased, pelagic and whole-lake NEP rates became more similar causing the residual NEP estimates to approach zero (Fig. 6c). This result suggests that benthic processes become less important for the net metabolic balance as lake area and water depth increased (Fig. 6; Table 2). Although not statistically significant, the benthic NEP estimate became more negative with increasing forest cover and was significantly negatively

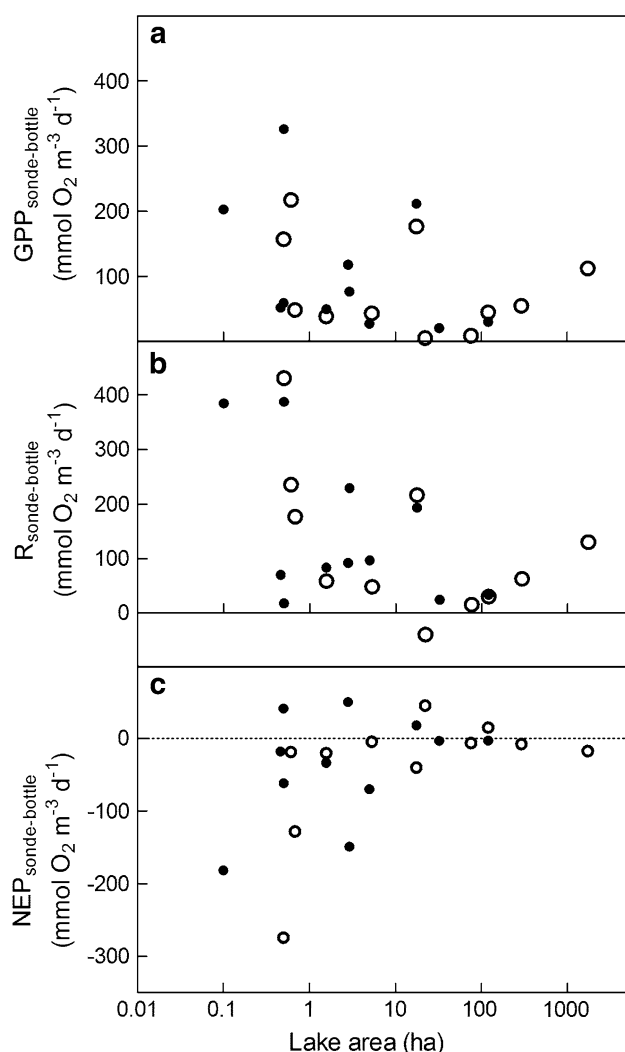


Fig. 6 Difference between sonde and bottle based metabolic rates and its relationships to lake area. The difference between whole-lake metabolic estimates, determined using the open water diel O_2 technique (sonde), and pelagic metabolism calculated from oxygen changes in bottles, is used to represent an effect of benthic metabolism. As lakes become larger, the effect of benthic metabolism (mainly respiration) becomes less important and the difference between NEP derived from sondes and bottles decreases. Data are averages over 6–8 days. *Filled circles* are fully-mixed lakes and *open circles* represent thermally stratified lakes

related to DOC concentration, suggesting that proportionally more oxygen was consumed by degradation of organic material in the benthic zone relative to oxygen production by primary production for forest lakes than for lakes located in open catchments.

The relative importance of lake meta-parameters and intrinsic biological and physical drivers for weekly averages of volumetric rates of GPP, R, and NEP was evaluated by multiple regression analysis. Among meta-parameters, mean lake depth was the best predictor of GPP and R, and both decreased with increasing water depth. A combination

of lake area and %forest cover was the best predictor of NEP (Table 3A). Light and temperature did not contribute significantly to explain between lake variability in GPP, R or NEP, suggesting that differences in these drivers were small and unimportant across the studied lakes during the study period (Table 3B). Algal biomass (Chl) was, as expected, the best predictor of GPP, while high rates of respiration and strong net heterotrophy ($NEP < 0$) were both related to high DOC (Table 3B). Evaluating the combined effect of meta-parameters and biological and physical conditions on weekly rates of whole lake metabolism, showed that GPP increased with higher algal biomass and lower water depth (Table 3C). Similarly, respiration increased with DOC and decreased with water depth. Variations in NEP were best explained by DOC, with no significant contributions from either lake size or forest cover. Thus, except for NEP, combining meta-parameters with internal biological drivers raised the overall explanatory power (r^2) of variations in lake metabolism by 14–15% to 57–63% (Table 3C).

Discussion

Overall, this study revealed strong broad-scale scaling patterns of lake metabolism and limnological properties to lake meta-parameters. With increasing lake area and depth, lakes received more light, were less wind exposed, had clearer water, deeper mixing depth and contained less nutrients and DOC, causing lakes to be less net heterotrophic and with less importance of benthic metabolism and less day-to-day variability in GPP. Also, with increasing forest cover lakes become shaded and less wind exposed, more humic and CO_2 rich, and more net heterotrophic. Meta-parameters were found to have as many significant, but usually weaker relationships, to whole-lake and benthic metabolism as the intrinsic drivers (TP, Chl and DOC) that are directly linked to photosynthesis and respiration. Combining water depth and Chl to predict GPP, and water depth and DOC to predict R, lead to stronger models of the variability of metabolism among the studied 25 lakes, stressing the importance of physical boundary conditions for lake performance.

Influence of lake size and forest cover on limnological properties

Physico-chemical features in 25 medium to high alkaline Danish lakes varied significantly with lake size and differences in forest cover of the catchments (Table 1). In agreement with previous studies, surface irradiance and wind exposure increased with lake surface area, but decreased with increasing shelter and shading from the

Table 3 Stepwise multiple linear regression models of volumetric ($\text{mmol O}_2 \text{ m}^{-3} \text{ day}^{-1}$) rates of GPP, R and NEP as a function of (A) Lake meta-parameters: lake area, mean water depth and %forest cover in the lake catchment, and (B) Biological and physical drivers: Chl, DOC, E_{mean} and water temperature, and (C) a combination of lake meta-parameters and, biological and physical drivers

Model type	Dependent variable	Parameter	Coefficient	t value	Overall r^2	Partial r^2	p
(A)	GPP	Depth	−0.83	−3.98	0.42		0.001
		Intercept	2.44	21.28			<0.0001
	R	Depth	−0.92	−4.56	0.49		0.001
		Intercept	2.62	23.47			<0.0001
	NEP	Size	0.02	2.66	0.39	0.20	0.015
		% forest	−0.03	−2.54		0.19	0.019
(B)	GPP	Intercept	3.00	147.35			<0.0001
		Chl	0.46	4.44	0.47		0.001
	R	Intercept	1.45	10.39			<0.0001
		DOC	0.89	4.93	0.52		<0.0001
	NEP	Intercept	1.28	6.88			<0.0001
		DOC	−0.08	−3.65	0.38		0.001
(C)	GPP	Intercept	3.06	133.51			<0.0001
		Chl	0.31	2.76	0.57	0.47	0.012
		Depth	−0.49	−2.23		0.10	0.037
	R	Intercept	1.87	8.21			<0.0001
		DOC	0.59	2.90	0.63	0.52	0.000
		Depth	−0.54	−2.48		0.11	0.022
	NEP	Intercept	1.85	6.54			<0.0001
		DOC	−0.08	−3.65	0.38		0.001
		Intercept	3.06	133.51			<0.0001

Analysis was performed on log-transformed data. Only parameters that fulfilled the required significance of $p < 0.05$ are shown, $n = 25$

forest surrounding the lakes (Fee et al. 1996; Sand-Jensen and Staehr 2007). Also, small surface areas were, as expected, statistically linked to shallow water and shallow mixing depth (Strasbaska 1980; Duarte and Kalff 1989; Fee et al. 1996). Our findings that small lakes are generally richer in nutrients, algal biomass, dissolved organic matter and CO_2 than large lakes located in the same surroundings, likewise agree well with previous broad-scale comparisons (Søndergaard et al. 2005; Sand-Jensen and Staehr 2007; Hanson et al. 2007; Nöges 2009).

Loading of DOC to lakes has previously been associated with the amount of wetlands in the watershed (Gergel et al. 1999), in particular wetlands with coniferous vegetation (Xenopoulos et al. 2003). The catchments of our study lakes had a small share of wetlands (0–7%), and DOC concentration was better related to the proportion of forest in the catchments, suggesting that regional models have limited applicability in predicting DOC in other geographical areas of the world (Xenopoulos et al. 2003). The strong influence of lake area and forest cover on lake DOC (Fig. 3a, b) supports two explanations. Firstly, hydrological input of DOC and nutrients across the terrestrial-aquatic boundary increases when the drainage ratio (catchment area to lake surface area) is high. Secondly, small lakes

possess a long shoreline for input of air-born terrestrial organic matter relative to lake surface area and volume and receive significant amounts of organic matter from litter fall (Gasith and Hasler 1976). The implications of higher DOC for physical and biological processes were firstly, shallower surface mixed layers and reduced light penetration (Snucins and Gunn 2000; Houser 2006) secondly, reduced planktonic production and increased planktonic respiration (Del Giorgio and Peters 1994), and finally, increased ecosystem respiration through mineralization of allochthonous organic carbon (Hanson et al. 2003; Staehr et al. 2010a).

The fluorescence index (FI) as derived by McKnight et al. (2001) suggested that not only does the amount of DOC vary notably across the studied lakes, but the quality (or origin) of the DOC varies as well (Fig. 3e, f). In agreement with expectations, we found that small lakes tend to contain more terrestrial material, whereas autochthonous production was a more important DOC source in larger lakes. The low FI in algal rich small lakes (Table 2) show that the terrestrial input of DOC is much higher than the input of DOC from degrading or leaking phytoplankton. Although large lakes do receive allochthonous DOC, its signal is overwhelmed by the production of

autochthonous DOC and the greater exposure to photochemical and microbial degradation as a result of longer residence times (Lindell et al. 2000).

Regulation of ecosystem metabolism by meta-parameters

Previous investigations on the influence of lake morphometry and catchment conditions on pelagic productivity of lakes has provided deviating conclusions. A global comparison of 55 shallow to deep lakes (1–730 m) showed that volumetric estimates of primary production decreased with increasing lake size, but was more strongly influenced by light and nutrient availability (Brylinsky and Mann 1973). In agreement with our findings (Fig. 2), studies in small to large lakes ($1\text{--}3 \times 10^6$ ha) by Duarte and Kalff (1989) found declining trophic and phytoplankton biomass with increasing area and mean depth. Work by Fee and co-workers on seven mid-sized to very large pristine lakes ($30\text{--}10^7$ ha), however, showed that lake size was a poor predictor of lake trophic and phytoplankton photosynthesis (Fee et al. 1992, 1996; Guildford et al. 1994). This response was explained by a greater turbulence and probability of nutrient regeneration within the mixed layer in very large lakes and greater upward nutrient flux (N and Si, but not P) across the thermocline. Also, in more recent studies of small lakes (0.02–20 ha), nutrients, algal biomass and CO_2 super saturation decreased with lake size, but no apparent scaling was found for pelagic metabolism (Sand-Jensen and Staehr 2007, 2009). Thus, previous studies on the importance of lake morphometry for primary productivity generally support our findings in small to mid-sized lakes (0.1–1,700 ha). However, relationships were weaker or inconsistent for the full range of lake sizes and relationships also depended on methodology. Earlier conclusions on lake metabolism were all based on bottle incubations, which only provide estimates of pelagic productivity. We used open water diel changes in DO to estimate whole-lake metabolism, which offer more reliable results and integrate pelagic and benthic processes under conditions of full vertical mixing (see more in Staehr et al. 2010b).

Forest lakes received less light and were expected to receive less easily accessible dissolved nutrients for phytoplankton production compared to lakes in fertilized agricultural landscapes (Larsen et al. 1994; Sand-Jensen and Staehr 2009). We therefore expected high forest cover to be associated with lower nutrient status, phytoplankton biomass and GPP in the lakes (Jackson and Hecky 1980). Nutrient levels were, however, similar for our open and forested lakes, and little differences in GPP were found between lakes of the same size but different forest cover. High inputs of organic material in forest lakes, on the other

hand, stimulate growth and metabolism of bacteria and zooplankton and enhance community respiration and constrain phytoplankton production due to greater background shading from colored DOC (Christensen et al. 1996; Jonsson et al. 2001; Sand-Jensen and Staehr 2007). Brown-colored small lakes in forest catchments were therefore significantly more net heterotrophic, in agreement with previous studies (Del Giorgio et al. 1999; Sand-Jensen and Staehr 2007, 2009). The high perimeter to area ratio for small lakes, coupled with high DOC flux and retention (Curtis and Schindler 1997) elevated carbon mineralization and net efflux of CO_2 to the atmosphere.

Influence of benthic processes on whole-lake metabolism

With increasing lake area, water depth tends to increase and the relative influence of benthic primary production can be expected to decrease as light becomes more limiting (Kemp et al. 1992). Although the importance of benthic primary producers is expected to be higher in shallow systems, poor light conditions associated with eutrophication may switch the dominance from benthic to pelagic processes (Vadeboncoeur et al. 2003). Our lakes were all placed in medium to high alkaline, nutrient-rich catchments, with relatively poor light conditions for benthic plant growth even in shallow lakes (See Table 1). Except for a few shallow lakes, most of our lakes had little submerged vegetation, and the benthic zone was accordingly dominated by carbon-rich and oxygen demanding sediments (author, pers obs), suggesting dominance of heterotrophic processes in the benthic environment. In support of this, we generally found higher sonde based (\sim whole-lake) than bottle based (\sim pelagic) respiration rates, especially so in small and shallow lakes (Table 2; Fig. 6b). Also the difference between sonde and bottle based NEP declined with increasing lake depth (Table 2) and area (Fig. 6c), indicating the influence of benthic processes on whole-lake metabolism to decrease with increasing lake size.

As shown in Coloso et al. (2011), diel changes in mixing depth and microstratification occurred in all of the lakes that were deep enough to stratify (12 out of 25). For these lakes, metabolic rates based on sonde measurements at shallow depth do not represent whole-lake estimates but rather the upper mixed layer (Coloso et al. 2008). The influence of benthic processes is therefore likely underestimated for our stratified lakes by a degree which depends on the volume of water below the mixed layer depth and the proportion of the lake bottom not being exposed to the upper mixed layer (Staehr et al. 2011), which in turn depends on lake morphometry and variability in mixing depth (Coloso et al. 2011). Applying hypsographic tables

for the stratified lakes, we find that 40–90% (mean 57%) of the lake volume and 20–70% (mean 53%) of the lake bottom is represented within the upper mixed layers of our stratified lakes. This suggests that a variable but likely substantial benthic signal is in fact included in our sonde-based estimates of metabolism in these lakes. Removing data from stratified lakes in our analysis (open circles in Fig. 6) would furthermore only weaken and not change relationships between the influence of benthic processes on lake metabolism and lake size.

Areal versus volumetric rates

In agreement with expectations, the implicit scaling was much weaker for areal than volumetric rates, and only GPP was significantly related to lake area (Table 2). Weak or absent relations to areal rates may derive from the confounding effect of co-variation of lake surface area and water depth. However, light utilization for photosynthesis per unit area is also known to be relatively similar among different plant communities and among systems of different depth (Krause-Jensen and Sand-Jensen 1998), and shallow lakes can accordingly be viewed as a compressed version of deeper lakes (Brylinsky and Mann 1973; Krause-Jensen and Sand-Jensen 1998) with little differences in areal rates of productivity.

Comparison of lake productivity amongst contrasting lakes can also be obtained by normalizing GPP to phytoplankton biomass, which serves as an index of the growth potential of algae (Staehr and Sand-Jensen 2007). For the lakes in this study, chlorophyll specific GPP decreased significantly with increasing TP concentration ($r = -0.42$, $p < 0.05$), while it increased with increasing mean light availability ($r = 0.47$, $p < 0.05$). These findings suggest that the efficiency of nutrient use of the autotrophic community increases with the degree of nutrient limitation, and that light availability is more important than nutrient availability for variation of primary production. Considering that the mean available irradiance (a function of surface irradiance, light attenuation and mixing depth) was unrelated to lake area and depth (Table 2), it is not surprising that areal rates of GPP, R and NEP show weak dependencies of lake morphometry.

Drivers of daily variability in metabolism

According to general scaling theory, the chemical and biological components of small aquatic systems are more variable as they are more sensitive to initial conditions, have limited external exchange of material and organisms with surroundings, and low buffering capacity (Kemp et al. 2001). Studies of scaling rules in aquatic ecosystems have furthermore shown that food chain length decreases with

reduced lake volume (Post et al. 2000) and these smaller lakes are less species rich, have less interspecies competition, and higher chance of rise and fall of populations.

In this study, daily variability of GPP declined with lake area and was highest in small nutrient rich and productive lakes. High productivity in nutrient-rich lakes is known to be associated with high day-to-day variability in GPP, R and NEP, and this is suggested to reflect the dynamic behavior of the lake ecosystem in response to changes in incident irradiance and available irradiance in the mixed surface layers (Staehr and Sand-Jensen 2007). High day-to-day variability in GPP in small lakes may also be impacted by changes of physical processes such as advection and inflow, and a greater influence from littoral metabolism (Vadeboncoeur et al. 2001). High variability of GPP also occurred in the small DOC rich lakes, which is somewhat counter intuitive. High input of DOC may restrict photosynthesis through greater competition for available light (Staehr et al. 2010a) and greater competition for nutrients among autotrophs and heterotrophs (Krause-Jensen and Sand-Jensen 1998) tend to reduce the temporal variability of metabolism. This stabilizing effect of DOC in forested lakes may also be due to the fact that DOC is a relatively time-stable energy source to bacteria and zooplankton (Cole et al. 2002). Thus, our results suggest that the stabilizing effect of DOC on GPP to be less influential than the destabilizing effects of high levels of nutrient, short food-chain length and stronger physical disturbance found in smaller sized lakes.

Our findings support the use of metabolic responses in lakes as a common metric that integrates terrestrial impacts on lake ecosystems (Williamson et al. 2008). The strong influence of lake morphometry and catchment conditions suggest that broad-scale comparisons among lakes and evaluation of their responses to human impacts (e.g., eutrophication, deforestation and climate change) need to take into account the strong implicit scaling with the physical boundary conditions. These operate directly through differences in shading, sheltering, physical mixing and indirectly through input of nutrients and organic matter.

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