

# Net Heterotrophy in Small Danish Lakes: A Widespread Feature Over Gradients in Trophic Status and Land Cover

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## ABSTRACT

Nineteen small lakes located in open landscapes or deciduous forests in nutrient-rich calcareous moraines in North Zealand, Denmark, were all net heterotrophic having negative net ecosystem production and predominant CO<sub>2</sub> supersaturation and O<sub>2</sub> undersaturation of lake waters. Forest lakes were poorer in nutrients, phytoplankton, and primary production, but richer in dissolved organic matter and CO<sub>2</sub> than open lakes with more light available. The modeled annual balance between gross primary production and community respiration ( $GPP/R_{COM}$ ) averaged 0.60 in forest lakes and 0.76 in open lakes and the ratio increased significantly with phosphorus concentration and phytoplankton biomass but decreased with colored dissolved organic matter. The negative daily rates of ecosystem production resembled estimates of oxygen uptake from the atmosphere to the lakes,

whereas estimates of CO<sub>2</sub> emission were 7.2-fold higher. Although CO<sub>2</sub>-rich groundwater and anaerobic respiration support greater molar release of CO<sub>2</sub> than uptake of O<sub>2</sub>, we suggest CO<sub>2</sub> emission is overestimated. Possible explanations include CO<sub>2</sub> enrichment of the air film above small wind-sheltered lakes. The observed metabolism and gas exchange show that exogenous organic matter is an important supplementary energy source to community respiration in these small lakes and that forest lakes, in addition, experience pronounced light attenuation from trees and dissolved colored organic matter constraining primary production.

**Key words:** lake; pond; forest cover; nutrients; whole-lake metabolism; heterotrophy; CO<sub>2</sub>-emission; O<sub>2</sub>-uptake.

## INTRODUCTION

Small lakes have several physico-chemical and biological features in common because small sur-

face areas statistically are linked to shallow water, wind shelter, and low mixing depth, while they possess a long shore line for input of airborne terrestrial organic matter relative to lake surface area and volume (Straskraba 1980; Duarte and Kaff 1989; Fee and others 1996). The hydrological input of organic matter and nutrients across the terrestrial-aquatic boundary is also high relative to surface area in lakes of similar character when the drainage ratio (catchment area/lake area) is high. Small lakes are, in addition, grossly influenced by

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Kaj Sand-Jensen (KSJ) formulated the original research idea and designed the study. Data analysis (ie. calculations, statistics and figures) was performed by Peter A. Staehr (PAS). The text was for the most part written by KSJ, although with contributions by PAS, especially in describing the applied methods and data analysis.

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shading from the terrestrial vegetation and by soil richness and land-use in the immediate surroundings (Sand-Jensen and Staehr 2007). In broad-scale comparisons of Danish lakes, small lakes are generally richer in nutrients, dissolved organic matter, and free CO<sub>2</sub> than large lakes located in the same surroundings (Søndergaard and others 2005; Sand-Jensen and Staehr 2007).

Small lakes in forest catchments have reduced inputs of light and easily accessible dissolved nutrients for phytoplankton production compared to lakes in fertilized agricultural landscapes (Larsen and others 1995). Forest cover should, therefore, be associated with lower nutrient status, phytoplankton biomass, and gross primary production (GPP) in the lakes (Jackson and Hecky 1980). Input of organic detritus from the forest, on the other hand, stimulates growth and metabolism of bacteria and zooplankton, enhances community respiration ( $R_{COM}$ ), and constrains phytoplankton production due to greater background shading from colored dissolved organic matter (CDOM; Christensen and others 1996; Krause-Jensen and Sand-Jensen 1998; Jonsson and others 2001, 2003). Consequently, brown-colored forest lakes should display stronger net heterotrophy than open, clear-water lakes (Del Giorgio and others 1999; Sobek and others 2002). Although increasing nutrient richness is believed to stimulate autotrophy more than heterotrophy (Cole and others 2000), input of easily degradable organic matter will have the opposite effect (Schindler and others 1997). It is, therefore, possible that small eutrophic lakes can still exhibit distinct net heterotrophy, but these aspects have not been thoroughly tested so far.

In this study, we compared phytoplankton biomass, particulate and dissolved organic matter, metabolic rates, and exchanges of CO<sub>2</sub> and O<sub>2</sub> with the atmosphere in small, alkaline seepage lakes in either predominantly open agricultural landscapes or deciduous forests in the rich moraine landscape in North Zealand, Denmark. Our main hypothesis was that these small, meso-eutrophic lakes can be net heterotrophic and release CO<sub>2</sub> to the atmosphere because of respiration of exogenous dissolved organic matter or processes related to this input. Our additional hypothesis was that nutrient concentration, phytoplankton biomass, and gross primary production are higher and dissolved organic matter and net heterotrophy are lower in open lakes than in forest lakes. Thus, supersaturation and emission of CO<sub>2</sub> to the atmosphere and undersaturation and influx of O<sub>2</sub> to the water as indices of net heterotrophy should be higher in forest lakes than in open lakes.

## MATERIALS AND METHODS

### Study Sites and Sampling

We examined 19 small, alkaline lakes (0.3–22 ha, median 10.5; 2.7–6.1 meq l<sup>-1</sup>, median 2.6) located in calcareous, nutrient-rich moraines near the town of Hillerød in North Zealand, Denmark (Table 1). Mean pH-values in surface waters ranged from 7.2 to 8.2 because of CO<sub>2</sub> supersaturation and were markedly lower than the pH of 8.2–8.5 attained at CO<sub>2</sub> equilibrium with atmospheric air (Stumm and Morgan 1996). Land use was determined from air photographs in a 200 m zone around the lakes. Forest cover ranged from 1% to 96% among the lakes. Lakes were fed by groundwater, rainwater, and intermittent surface flow and, except for three lakes (that is, Slotssø, Teglgårdssø, and Strødam Engsø) they lacked permanent stream inputs. Water residence time and loading with organic matter and nutrients were not known for most lakes. In small forest lakes, shed leaves were the main input of exogenous particulate organic matter. All lakes were shallow with mean depths ranging from 1 to 3.5 m. The water had measured mean vertical light attenuation coefficients ( $K_D$ , 400–700 nm) ranging from 1.0 to 5.2 m<sup>-1</sup> (Table 1). Light attenuation coefficients in all lakes on all sampling dates were calculated from measurements (see below) of total suspended dry matter (TSM), algal biomass (Chl *a*), and absorbance of colored dissolved organic matter (CDOM) by applying the optical model described in Sand-Jensen and Staehr (2007). Small lakes surrounded by tall forest trees experience very pronounced shading from the trees. The reduction of surface irradiance (SI) has previously been quantified in the region as a function of lake size across the size range studied here (Sand-Jensen and Staehr 2007). This model was used to calculate surface irradiance in the present set of lakes.

### Water Chemistry, Clarity, and Phytoplankton Pigments

Lakes were sampled eight times from November 2000 to November 2001. All physico-chemical and biological measurements were made in triplicate. Water temperatures were between 1°C and 24°C during this period and lakes were ice-free during sampling. Temperature was measured and water sampled at 0.3 m depth in the center of the homogeneously mixed lakes between 10 and 12 o'clock. Water for chemical and physical measurements was transferred to 10 l plastic containers and analyzed on the same day or frozen for later anal-

**Table 1.** Surface Area and Mean Depth of the 19 Small Danish Lakes and Forest Cover Measured in a 200 m Wide Zone Along the Lake Shore

Lake	Size (m <sup>2</sup> )	Mean depth (m)	Forest cover (%)	pH	ANC (meq l <sup>-1</sup> )	Chl <i>a</i> (µg l <sup>-1</sup> )	TN (µg l <sup>-1</sup> )	TP (µg l <sup>-1</sup> )	K <sub>D</sub> (m <sup>-1</sup> )	TSM (mg l <sup>-1</sup> )
Agertofte	6,061	1	58	7.2 ± 0.1	2.2 ± 0.1	11.7 ± 2.8	1040 ± 20	72 ± 10	4.1 ± 0.2	2.8 ± 0.5
Badstuedam	28,039	1	46	8.2 ± 0.2	2.8 ± 0.2	14.2 ± 3.4	836 ± 72	52 ± 4	1.3 ± 0.1	3.4 ± 0.6
Bendstrup Sø	2,615	1	1	7.6 ± 0.3	2.4 ± 0.1	101.3 ± 29.1	1575 ± 221	285 ± 43	2.4 ± 0.3	11.3 ± 3.2
Brededam	2,2719	1.3	73	7.5 ± 0.1	2.9 ± 0.1	12.7 ± 1.6	522 ± 52	51 ± 18	1.4 ± 0.2	2.7 ± 0.2
Bøllelose	4,601	0.8	11	7.8 ± 0.1	3.3 ± 0.2	43.9 ± 8.7	699 ± 64	48 ± 3	1.5 ± 0.1	13.7 ± 4.7
Favrholm Sø	1,0476	1.5	1	7.9 ± 0.2	2.4 ± 0.2	20.7 ± 6.0	819 ± 53	67 ± 17	1.3 ± 0.2	9.3 ± 3.4
Fønstrup dam	6,826	1.6	96	7.4 ± 0.2	2.7 ± 0.1	19.6 ± 5.2	794 ± 60	55 ± 6	2.0 ± 0.2	4.8 ± 1.2
Hesteskodam	5,246	1.5	30	7.5 ± 0.1	1.6 ± 0.0	40.6 ± 6.3	1332 ± 126	93 ± 11	2.1 ± 0.4	9.2 ± 2.9
Karlso	2,9082	1.1	49	7.3 ± 0.0	2.1 ± 0.1	27.0 ± 9.8	986 ± 86	96 ± 9	5.2 ± 0.5	3.9 ± 0.7
Præstevang Kirke Sø	6,763	1.5	23	7.6 ± 0.1	2.7 ± 0.1	19.0 ± 7.3	756 ± 50	47 ± 7	1.6 ± 0.2	3.4 ± 0.6
Selskovsvej Sø	22,876	3	43	7.7 ± 0.1	3.7 ± 0.1	14.9 ± 3.9	963 ± 94	82 ± 13	1.1 ± 0.1	4.8 ± 1.5
Slotssø	220,728	3.5	15	8.1 ± 0.2	2.6 ± 0.1	52.6 ± 42.2	945 ± 153	192 ± 23	1.5 ± 0.4	9.9 ± 5.4
Sortedam	5,028	1.2	29	7.1 ± 0.1	1.2 ± 0.1	38.7 ± 11.1	1236 ± 289	109 ± 38	2.5 ± 0.2	9.6 ± 3.7
Sortedam v. C. vej	3,942	1	48	7.4 ± 0.1	2.6 ± 0.2	12.3 ± 1.3	585 ± 42	70 ± 26	1.6 ± 0.1	3.6 ± 0.4
Spejldam	3,755	1	42	7.8 ± 0.1	2.6 ± 0.0	31.3 ± 12.1	955 ± 188	168 ± 130	1.0 ± 0.2	7.9 ± 3.1
Store Funkedam	15,643	1.5	72	7.5 ± 0.1	2.1 ± 0.2	8.1 ± 0.6	577 ± 26	25 ± 4	1.9 ± 0.1	3.0 ± 0.8
Strødam Engssø	175,730	1	27	7.9 ± 0.1	5.4 ± 0.4	13.7 ± 5.4	2489 ± 1097	306 ± 51	1.7 ± 0.2	12.2 ± 3.7
Teglårdssø	53,177	1	34	7.5 ± 0.1	2.3 ± 0.1	21.0 ± 3.0	954 ± 23	54 ± 17	2.9 ± 0.2	8.3 ± 2.9
Ødam	31,249	1	38	8.1 ± 0.1	3.1 ± 0.1	21.1 ± 5.1	668 ± 47	67 ± 18	1.2 ± 0.1	4.8 ± 1.2

Characteristics of the surface waters including pH, alkalinity (ANC, acid neutralizing capacity), chlorophyll *a* concentration, total-nitrogen (TN), total-phosphorus (TP), vertical light attenuation coefficient (K<sub>D</sub>), and total suspended matter (TSM) are also given. Mean values ± SE.

yses of total-nitrogen (TN) and total-phosphorus (TP) according to Strickland and Parsons (1968). Total suspended dry matter (TSM) was determined by filtration on pre-weighed GF/C-filters followed by drying at 105°C and weighing. The filtrate was further filtered ( $<0.2\ \mu\text{m}$ ) to remove bacteria and other fine particles and absorbance of colored dissolved organic matter (CDOM) was measured at several wavelengths (340–460 nm) in a 5-cm cuvette in a Shimadzu spectrophotometer (UV-160A) and expressed as CDOM absorption ( $\text{m}^{-1}$ ) as recommended by Cuthbert and del Giorgio (1992) and Kirk (1994) by multiplying with 2.3 (from  $\log_{10}$  to  $\log_e$ ) and dividing by the optical path length (0.05 m). CDOM absorption at 360 nm is presented here, whereas the highly reproducible logarithmic decline of absorption from 340 to 460 nm was used to calculate mean absorption for the photosynthetic range (400–700 nm) in the optical model (Sand-Jensen and Staehr 2007). In comprehensive measurements from Danish eutrophic lakes and streams, DOC concentrations ( $\text{mg C l}^{-1}$ ) increased linearly with CDOM absorption at 360 nm ( $\text{m}^{-1}$ ) according to the equation:  $\text{DOC} = 0.454 \text{CDOM}_{360} + 1.9$  ( $r^2 = 0.80$ ,  $n = 399$ , Stedmon, unpublished). Samples for chlorophyll *a* and pheopigments were collected on Advantec® GC-50 filters, extracted with 96% ethanol for 24 h and measured according to the method described by Parsons and others (1984).

## Metabolism and Gas Exchange

Measurements just before noon approximately represent the daily average concentrations of  $\text{CO}_2$  and  $\text{O}_2$  (Sand-Jensen and Staehr 2007). Water for determination of  $\text{O}_2$ , pH, and calculations of  $\text{CO}_2$  was transferred to closed, dark glass bottles to avoid  $\text{CO}_2$  and  $\text{O}_2$  exchange with the air and prevent photosynthesis before measurement in the laboratory within 2 h. pH was measured with radiometer equipment (accuracy 0.01 pH unit) and  $\text{O}_2$  with stirring insensitive Clark-type microelectrodes (Unisense; accuracy  $0.01\ \text{mg O}_2\ \text{l}^{-1}$ ). Measurements of ionic strength, alkalinity, and pH were used to calculate concentrations of free  $\text{CO}_2$  according to Rebsdorf (1972). The calculated  $\text{CO}_2$  concentrations have previously been shown to be in close agreement with direct  $\text{CO}_2$  measurements on an IRGA using a headspace equilibration technique (Sand-Jensen and Frost-Christensen 1998). The pH-alkalinity approach was used because we were able to analyze the large number of samples with better reproducibility than by the IRGA approach.

Percent saturation of  $\text{O}_2$  and  $\text{CO}_2$  was calculated as the ratio of the measured gas concentration and the gas concentration in water in equilibrium with the atmosphere at ambient temperature. A standard table was used to compute oxygen saturation from water temperature.  $\text{CO}_2$  saturation was calculated as a function of mean  $\text{CO}_2$  partial pressure (380 ppm) in air at the time of investigation and water temperature according to Plummer and Busenberg (1982).

Gas fluxes of  $\text{O}_2$  and  $\text{CO}_2$  across the air–water interface were calculated as the product of the gas exchange coefficient (piston velocity,  $k$ ,  $\text{cm h}^{-1}$ ) and the concentration gradient:  $D = k ([\text{gas}]_{\text{meas}} - [\text{gas}]_{\text{sat}})$ . Piston velocity was estimated from  $k_{600}$  and the ratio of Schmidt numbers as  $k = k_{600} * ((Sc/600)^{-0.5})$  according to Jahne and others (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:  $k_{600}\ (\text{cm h}^{-1}) = 2.07 + 0.215\text{wind}^{1.7}$  according to Cole and Caraco (1998). Measurements during several years in some of these small lakes have confirmed that wind speed is indeed low ( $0\text{--}3\ \text{m s}^{-1}$ ) for more than 90% of the time (Closter 2007). We therefore applied a wind speed of  $2\ \text{m s}^{-1}$  for all dates. The flux equation for  $\text{CO}_2$  is analogous to that of  $\text{O}_2$  but includes a factor,  $\alpha$ , which represents the chemical enhancement of diffusion, which occurs at high pH and during low wind speeds when the stagnant layer is thick. We used the approach in Bade and Cole (2006) to compute  $\alpha$ .

Metabolic rates in the pelagic waters were measured in triplicate by standard oxygen experiments in closed glass bottles (25 ml) mounted on a rotating wheel in a temperature-constant incubator set at ambient temperature. Net oxygen production at light saturation ( $\text{NP}_{\text{max}}$ ) of the plankton community was determined as the increase of oxygen concentrations in the water exposed to a saturating irradiance of  $400\ \mu\text{mol photons m}^{-2}\ \text{s}^{-1}$  for 6–18 h. Respiration of the plankton ( $R$ ) was measured as the decline of oxygen concentrations in dark bottles for 18–42 h. Long incubations were used when rates were lowest. Oxygen concentrations were measured using the microelectrode equipment. Gross primary production at light saturation ( $\text{GPP}_{\text{max}}$ ) was calculated in the conventional way as the sum of  $\text{NP}_{\text{max}}$  and  $R$  assuming that dark respiration continues at unaltered rates in the light.

Benthic respiration was measured in triplicate sediment cores retrieved in Kajak Perspex cylinders (5.2 cm in diameter) from the central part of the lakes in April–May and incubated in the dark at  $12^\circ\text{C}$  for 1–2 days. Oxygen consumption was

determined as the rate of decline of dissolved O<sub>2</sub> in the enclosed water volume overlying the sediment. Water was stirred by a magnetic stirrer bar during incubation. Benthic respiration was corrected for respiration in the water overlying the sediment cores by parallel incubation of water alone. Benthic respiration measurements were assumed to be representative for the entire lake and the full year. This is obviously a crude assumption which does not account for spatial and temporal variability in the amount of labile organic matter. We regard the incubation temperature of 12°C as a suitable choice because if respiration rates change with temperature with a standard Q<sub>10</sub>-value of 2.0, annual means of respiration rates corrected to monthly temperatures over the year available for two lakes in the region (Closter 2007) yielded values within ±5% of the value at 12°C.

Total daily lake respiration ( $R_{\text{COM}}$ ) was calculated by multiplying hourly rates of volumetric pelagic respiration with 24 h and mean water depth and adding benthic respiration. Pelagic waters were usually well mixed and had little spatial variability, whereas greater spatial variability is expected for benthic respiration which may, as already mentioned, generate uncertainty by up-scaling to the entire lake ecosystem. Total daily gross primary production (GPP) was calculated from maximum light-saturated gross production in the pelagic waters ( $GP_{\text{max}}$ , mol O<sub>2</sub> m<sup>-3</sup> h<sup>-1</sup>), the attenuation coefficient ( $K_D$ , m<sup>-1</sup>), number of light hours per day (LDH, h day<sup>-1</sup>, Jensen 2000) according to the empirical model of Talling 1957, (his Eq. 5), but modified to correct for forest shading by multiplying by mean irradiance at the lake surface as a proportion of irradiance in the open (SI):

$$\text{GPP} = GP_{\text{max}}(\ln 2 / 1.33K_D) \times \text{LDH} \times \text{SI}$$

Daily rates were integrated over the year by linear interpolation between successive measurements. The contribution of submerged macrophytes and benthic microalgae was not included in our estimate of ecosystem production. Emergent macrophytes were present in shallow water of the lakes but they exchange O<sub>2</sub> and CO<sub>2</sub> with the atmosphere during their photosynthetic production, whereas they decompose in the water upon senescence like the input of terrestrial organic matter. The growth of submerged macrophytes was negligible in most lakes. There will, however, be a certain contribution of benthic microalgae to ecosystem production (Vadeboncoeur and others 2001, 2003), although high shading from forest trees surrounding the small lakes and high light

attenuation in the plankton-rich and brown-colored water will restrict this productivity as well. Thus, we acknowledge that ecosystem GPP and GPP/R values are probably underestimated by not including the benthic production of microalgae.

## Statistics

To determine the correlations between forest cover, season, physico-chemical and biological variables a Pearson correlation matrix was established. To specifically evaluate the influence of forest cover and season, lakes were first divided into 11 predominantly open lakes (1–42% forest cover, median 27%) and 8 predominantly forest lakes (50–96% forest cover, median 64%) with no overlap in forest cover between the two groups and no difference in lake size. Data were log-transformed, when necessary, to fulfill the requirements of parametric analysis.

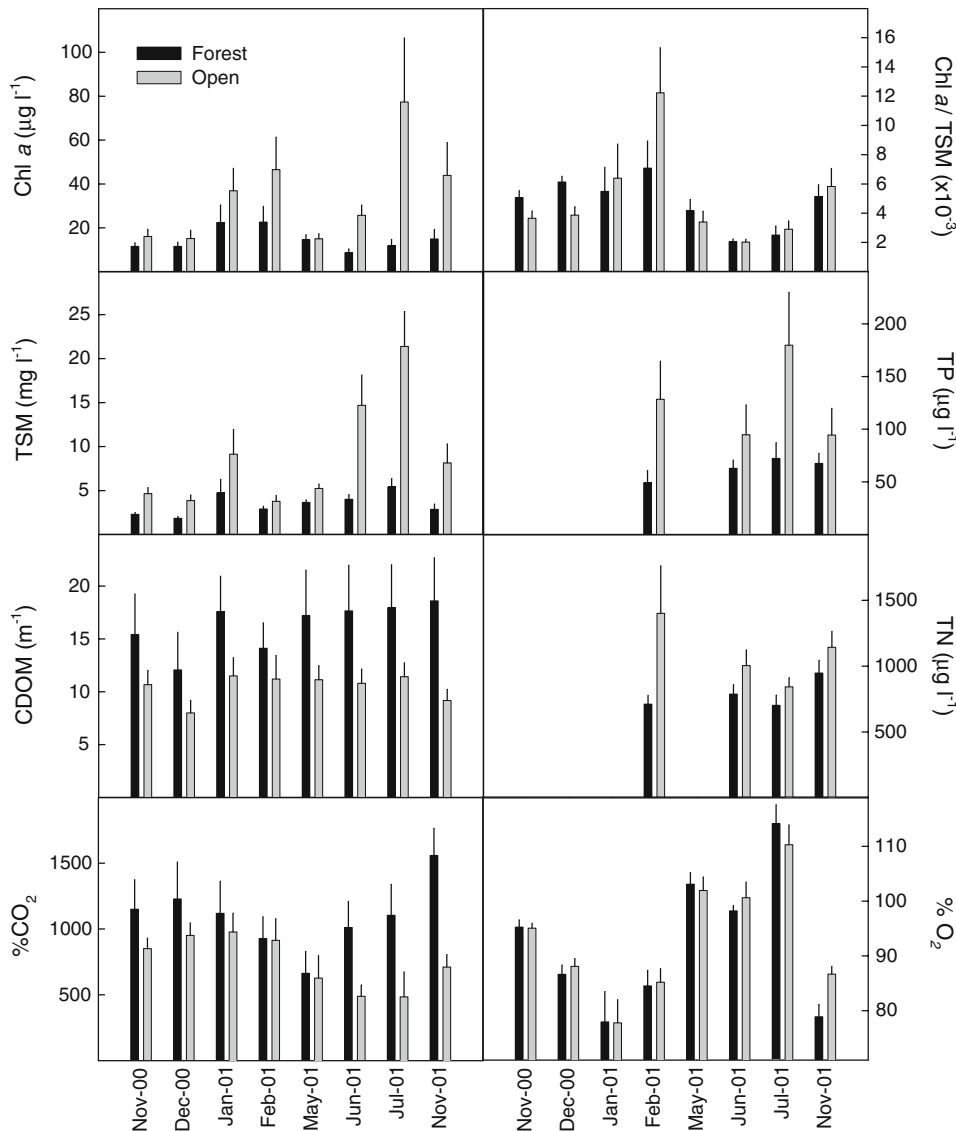
## RESULTS

### Water Chemistry, Organic Matter, and Forest Cover

All 19 small lakes had high nutrient concentrations (seasonal means: 25–285 µg TP l<sup>-1</sup>, 521–2489 µg TN l<sup>-1</sup>) and phytoplankton biomasses (seasonal means: 8–100 µg Chl l<sup>-1</sup>) corresponding to mesotrophic to very eutrophic conditions (Figure 1). Nutrient concentrations (TN and TP) were higher ( $P < 0.088$ ) in open lakes than in shaded forest lakes (Figure 1) and negative correlations of nutrient concentrations to forest cover among lakes were significant (Table 2). Total suspended matter (TSM) and phytoplankton biomass (Chl *a*) in pelagic water declined significantly with higher forest cover, whereas CDOM absorption, CDOM/Chl *a*, and free CO<sub>2</sub> concentrations increased (Table 2). Phytoplankton biomass increased significantly with TP (Table 2).

All lakes were strongly supersaturated with CO<sub>2</sub> during autumn and winter, whereas CO<sub>2</sub> supersaturation during summer was weaker (Figure 1). CO<sub>2</sub> concentrations were lowest in forest lakes in early May and in open lakes in June–July. Among eight forest lakes, 97% of CO<sub>2</sub> measurements displayed supersaturation with an annual median value of about 975% air saturation. Among 11 open lakes, 87% of the measurements showed CO<sub>2</sub>-supersaturation and the annual median value was about 710% air saturation. O<sub>2</sub> concentrations in surface waters were greatly undersaturated during autumn and winter, close to atmospheric





**Figure 1.** Seasonal variations in forest lakes and open lakes of phytoplankton (Chl), total suspended matter (TSM and Chl/TSM), colored dissolved organic matter (CDOM), total nutrients (TP and TN), and % saturation of  $\text{CO}_2$  and  $\text{O}_2$ . Mean values ( $\pm$ SE) are shown.

equilibrium in May and June, and only supersaturated in July (Figure 1). Forest lakes and open lakes were undersaturated with  $\text{O}_2$  in 75% of measurements. The extent of  $\text{CO}_2$  supersaturation was significantly positively correlated with the extent of  $\text{O}_2$  undersaturation (Table 2).

Concentrations of free  $\text{CO}_2$  declined significantly with TSM and increased highly significantly with CDOM absorption according to a hyperbolic relationship (Table 2, Figure 2). The range of mean CDOM absorption ( $6\text{--}34\text{ m}^{-1}$ ) among the lakes corresponds to dissolved organic carbon concentrations (DOC) between approximately 4 and  $18\text{ mg C l}^{-1}$  according to the general empirical relationship of DOC to CDOM absorption (see section “Materials and Methods”). In multiple regression analyses (log transformed data) only the

positive relationship to CDOM contributed significantly to the prediction of daily mean  $\text{CO}_2$  concentrations, whereas the positive influence of forest cover and the negative influence of phytoplankton biomass were not significant but may exert their influence through inter-correlations with CDOM.

## Production and Respiration

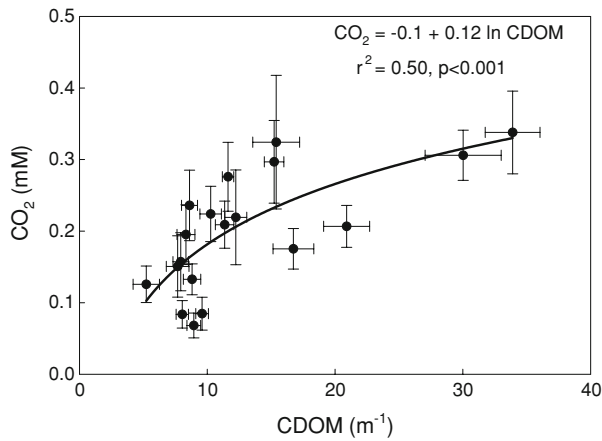
For the entire lake ecosystem, daily gross primary production (GPP) and community respiration ( $R_{\text{COM}}$ ) were significantly positively related to TP, Chl *a*, and TSM (Table 2).  $R_{\text{COM}}$  increased along with GPP, being a main source of respiratory substrates, and in most cases  $R_{\text{COM}}$  exceeded GPP (Figure 3). Benthic respiration was responsible for  $44 \pm 5\%$  (mean  $\pm$  95% CL) of community respi-

**Table 2.** Pearson Correlation Coefficients Among Forest Cover, Nutrients (TP and TN), Limnological Variables (Chl *a*, Temperature, TSM, CDOM, and CDOM/Chl *a*), Gas Concentrations and Exchange Rates of CO<sub>2</sub> and O<sub>2</sub>, and Metabolic Properties (GPP, *R*<sub>COM</sub> and GPP/*R*<sub>COM</sub>) for 19 Lakes on 8 Days During the Year

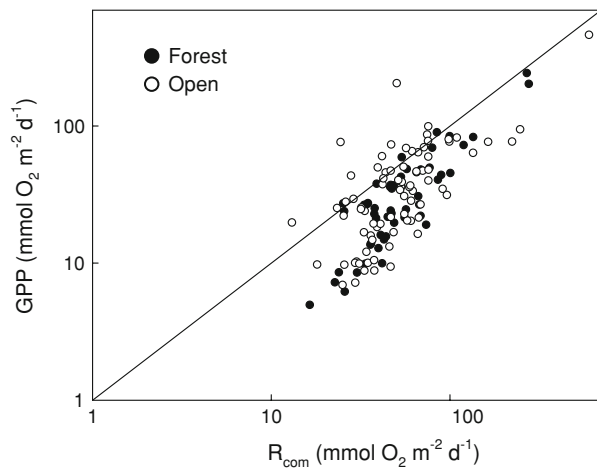
	TP	TN	Chl <i>a</i>	TSM	CDOM	CDOM/Chl <i>a</i>	Temp	%CO <sub>2</sub>	%O <sub>2</sub>	CO <sub>2</sub> flux	O <sub>2</sub> flux	GPP	<i>R</i> <sub>COM</sub>	GPP/ <i>R</i> <sub>COM</sub>
%Forest	-0.36**	-0.28*	-0.27**	-0.32**	0.26**	0.37***	-0.01	0.21*	-0.09	0.19*	-0.09	-0.04	0.01	-0.07
TP		0.61***	0.32***	0.46***	0.06	-0.25*	0.13	-0.10	-0.19	0.08	0.19	0.41***	0.32**	0.23*
TN			0.18	0.18	0.06	-0.13	-0.07	0.16	-0.19	0.16	-0.19	0.02	0.06	-0.04
Chl <i>a</i>				0.59***	-0.07	-0.88***	-0.17*	-0.15	-0.02	-0.13	-0.01	0.32***	0.25**	0.24**
TSM					-0.06	-0.53***	0.28***	-0.30***	0.28***	-0.25**	0.29***	0.47***	0.30***	0.41***
CDOM						0.54***	-0.03	0.33***	-0.85***	0.48***	-0.05	-0.09	0.02	-0.17*
CDOM/Chl <i>a</i>							0.16	0.29***	-0.01	0.34***	-0.01	-0.31***	0.20*	-0.28**
Temp								-0.24**	0.64***	-0.11	0.65***	0.23**	-0.07	0.43***
%CO <sub>2</sub>									-0.49***	0.87***	-0.50***	-0.37***	-0.18*	-0.38***
%O <sub>2</sub>										-0.46***	0.99***	0.48***	0.24**	0.48***
CO <sub>2</sub> -flux											-0.46***	-0.29***	-0.14	-0.31***
O <sub>2</sub> -flux												0.53***	0.29***	0.49***
GPP													0.74***	0.70***
<i>R</i> <sub>COM</sub>														0.04

Analyses were performed on log-transformed data.

\*\*\**P* < 0.001, \*\**P* < 0.01, \**P* < 0.05.



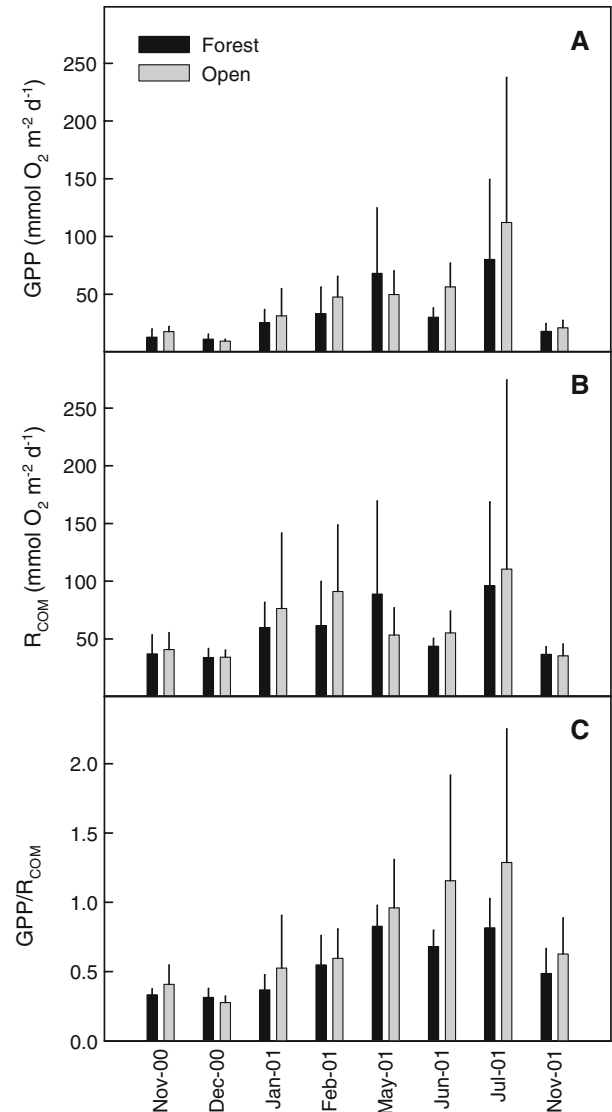
**Figure 2.** Daily mean  $\text{CO}_2$  concentration in 19 small lakes over the year as a function of mean CDOM absorption. Error bars are standard errors.



**Figure 3.** Relationship between daily gross primary production and community respiration in forest lakes (closed circles) and open lakes (open circles). The line shows GPP equal to  $R_{\text{COM}}$  and zero net community production. The GM-regression line follows the equation:  $\log \text{GPP} = 1.04 \log R_{\text{COM}} - 0.30$  ( $r^2 = 0.55$ ,  $P < 0.0001$ ).

ration in open lakes and  $37 \pm 5\%$  in forest lakes, whereas pelagic respiration accounted for the remainder. The  $\text{GPP}/R_{\text{COM}}$ -ratio declined with forest cover (Table 2), but the difference between forest lakes and open lakes was only significant when seasonal changes were accounted for (data not shown). The  $\text{GPP}/R_{\text{COM}}$ -ratio increased significantly with TP, TSM, and phytoplankton biomass, and declined significantly with CDOM and CDOM/Chl *a* (Table 2).

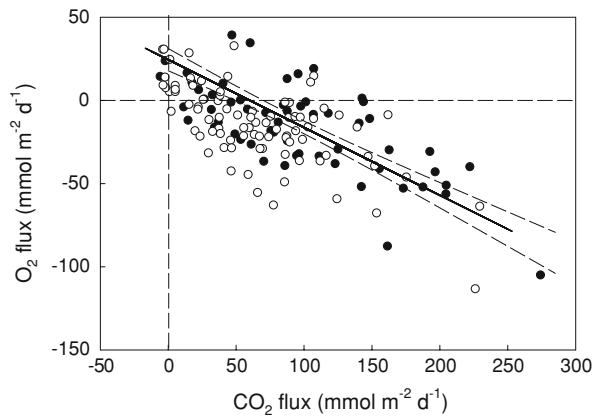
Gross primary production was much higher during summer than during autumn and winter (Figure 4). Although community respiration dis-



**Figure 4.** Seasonal variations of daily rates of gross primary production (GPP, panel A), community respiration ( $R_{\text{COM}}$ , panel B), and the ratio between them (panel C) in forest lakes and open lakes. Mean values ( $\pm \text{SE}$ ).

played the same overall seasonal pattern, differences between summer and winter were less pronounced (Figure 4). This is in part due to the application of a constant sediment respiration, but seasonal changes in the pelagic community were also larger for phytoplankton net production (coefficient of variation, CV: 61%) than plankton community respiration (CV: 48%). Annual means of  $\text{GPP}/R_{\text{COM}}$  were higher in open lakes (avg. 0.76) than forest lakes (0.60) and the ratios were lowest during autumn and winter in both lake types and higher than 1.0 only during summer in open lakes (Figure 5).





**Figure 5.** Relationship between daily estimated fluxes of  $\text{CO}_2$  and  $\text{O}_2$  ( $\text{mmol m}^{-2} \text{d}^{-1}$ ) across the air–water interface of eight forest lakes (closed circles) and eleven open lakes (open circles) at eight different times during the year. Positive values are effluxes. The geometric mean regression is:  $\text{O}_2\text{-flux} = 24.5 - 0.41 \text{ CO}_2\text{-flux}$  ( $r^2 = 0.19$ ,  $P < 0.01$ ).

### Gas Fluxes and Net Heterotrophy

Net heterotrophy was prominent as most of the lakes were supersaturated with  $\text{CO}_2$ , undersaturated with  $\text{O}_2$ , and had  $\text{GPP}/R_{\text{COM}}$ -ratios below 1.0 during most of the year (Figures 1 and 4). Estimated  $\text{CO}_2$  emissions were higher during autumn–winter than summer and annual mean  $\text{CO}_2$  emission was  $43.0 \text{ mol m}^{-2} \text{y}^{-1}$  in forest lakes and  $27.3 \text{ mol m}^{-2} \text{y}^{-1}$  in open lakes (Table 3). Estimated influxes of  $\text{O}_2$  were complementary to  $\text{CO}_2$  emissions being higher during autumn–winter than summer and annual values were slightly higher in forest lakes ( $5.1 \text{ mol O}_2 \text{ m}^{-2} \text{y}^{-1}$ ) than in open lakes ( $4.4 \text{ mol O}_2 \text{ m}^{-2} \text{y}^{-1}$ ). A highly significant inverse relationship was observed between  $\text{CO}_2$  and  $\text{O}_2$  fluxes among lakes over time in accordance with the complementary role of the two gases in photosynthesis and aerobic respiration (Figure 5). It is noteworthy, that a positive  $\text{CO}_2$ -efflux was estimated at

a zero  $\text{O}_2$ -flux and that the slope of  $\text{O}_2$ -flux versus  $\text{CO}_2$ -flux was  $-0.41$  and significantly less negative than  $-1.0$  implying that, on a molar basis, estimated  $\text{CO}_2$  emission was much higher than estimated  $\text{O}_2$  uptake.

Emission of  $\text{CO}_2$  and uptake of  $\text{O}_2$  both increased with falling  $\text{GPP}/R_{\text{COM}}$ -ratio and more negative net ecosystem production ( $\text{NEP} = \text{GPP} - R_{\text{COM}}$ ). The absolute rate of  $\text{O}_2$  uptake from the atmosphere into the lakes is at the same level as the negative net ecosystem production, whereas the rate of  $\text{CO}_2$  emission is much greater than what the surplus of community respiration can account for (Table 3).

## DISCUSSION

### Influence of Forest Cover and Dissolved Organic Matter

The small lakes examined here exhibited significantly declining concentrations of nutrients and phytoplankton biomass with greater forest cover, whereas CDOM absorption and  $\text{CO}_2$  supersaturation increased (Table 2). Input of soil nutrients is generally much lower in lakes located in forests than in open lakes located in cultivated landscapes (Larsen and others 1995). Input of leaves and dissolved organic matter, on the other hand, is high from forested catchments and can support microbial growth and microbial respiration in forest lakes contributing to their profound  $\text{CO}_2$  supersaturation (Tranvik 1992). These conditions can account for the observed differences between forest lakes and open lakes. In addition, extra input of dissolved organic matter will impede phytoplankton biomass due to the enhanced background light attenuation which competes with phytoplankton pigments for available light as shown by phytoplankton growth models and laboratory tests under nutrient replete conditions (Huisman and Weissing 1994; Krause-Jensen and Sand-Jensen 1998). In Long Lake, Wisconsin, for example, an increase of refractory

**Table 3.** Annual Rates of Metabolism and Gas Exchange Rates in 8 Predominantly Forest Lakes and 11 Predominantly Open Lakes

Parameter	Forest lakes	Open lakes
Gross primary production ( $\text{GPP}$ , $\text{mol O}_2 \text{ m}^{-2} \text{y}^{-1}$ )	$11.9 \pm 6.5$	$14.1 \pm 5.8$
Community respiration ( $R_{\text{com}}$ , $\text{mol O}_2 \text{ m}^{-2} \text{y}^{-1}$ )	$22.0 \pm 7.7$	$22.7 \pm 7.9$
Net ecosystem production ( $\text{NEP}$ , $\text{mol O}_2 \text{ m}^{-2} \text{y}^{-1}$ )	$-10.1 \pm 2.1$	$-8.7 \pm 3.8$
$\text{GPP} : R_{\text{com}}$	$0.60 \pm 0.07$	$0.76 \pm 0.16$
$\text{O}_2$ exchange rate ( $\text{mol O}_2 \text{ m}^{-2} \text{y}^{-1}$ )	$-5.1 \pm 2.9$	$-4.4 \pm 2.6$
$\text{CO}_2$ exchange rate ( $\text{mol CO}_2 \text{ m}^{-2} \text{y}^{-1}$ )	$43.0 \pm 15.0$	$27.3 \pm 8.3$

Mean  $\pm$  95% CL.

DOC from 5 to 17 mg l<sup>-1</sup>, resembling the DOC range in our lake comparison, was estimated to reduce phytoplankton biomass and primary production corresponding to a 10-fold decline of the external P-loading rate (Carpenter and others 1998) because higher phytoplankton biomass (and more P) is required to absorb the same proportion of incident irradiance. In our lake comparison, CDOM absorption was negatively related to GPP/ $R_{\text{COM}}$  (Table 2). The quotient CDOM/Chl *a* directly reflects the competition between background absorption and photosynthetic pigment absorption (Krause-Jensen and Sand-Jensen 1998) and it was significantly negatively related to GPP and GPP/ $R_{\text{COM}}$  (Table 2). We, therefore, agree with Pace and others (2007) that CDOM/Chl *a* could be a suitable and easily measurable predictor of the balance between allochthonous and autochthonous carbon to plankton consumers.

## Lake Metabolism and Net Heterotrophy

Community respiration exceeded gross primary production in all lakes stressing the net heterotrophic character of both nutrient-rich open lakes and forest lakes with high input of allochthonous organic carbon. Exogenous organic substrates offer an additional source to  $R_{\text{COM}}$  that may explain why CO<sub>2</sub> is emitted to the atmosphere and O<sub>2</sub> is taken up and why their magnitudes are positively related to CDOM (Table 2, Figure 2). This finding corresponds well with the positive relationship of CO<sub>2</sub> to DOC of boreal lakes (Sobek and others 2005).

Gross primary production and community respiration both increased significantly under more nutrient-rich conditions in lakes having high phosphorus and chlorophyll concentrations (Table 2). The close relationship of community respiration to phytoplankton biomass and production (Table 2, Figure 3) can result from a direct role of phytoplankton in the respiratory budget and an indirect role when phytoplankton carbon is consumed by bacteria and animals. GPP increased more than  $R_{\text{COM}}$  by increasing nutrient richness supporting earlier suggestions of greater stimulation of autotrophy than heterotrophy (Schindler and others 1997; Cole and others 2000; Duarte and Prairie 2005). Uptake of O<sub>2</sub> from the atmosphere declined under more nutrient-rich conditions, though not significantly ( $P = 0.10$ ).

It is noteworthy that net ecosystem production remained negative in both open lakes (-8.7) and forest lakes (-10.1 mol O<sub>2</sub> m<sup>-2</sup> y<sup>-1</sup>) consistent with GPP/ $R_{\text{COM}}$  annual means of 0.76 and 0.60, respectively (Table 3). These annual balances are

estimated by a combined optical-photosynthesis model using measurements of pelagic metabolism and attenuating TSM, CDOM, and Chl *a* on eight occasions during the year, but only one measurement series of benthic respiration. No contribution of benthic production was included. Despite these uncertainties, the calculations gain credibility by showing the same systematic pattern among lakes that all had negative NEP-values and of the same magnitude as O<sub>2</sub> influx from the atmosphere calculated independently.

Predominantly negative net ecosystem productivity is associated with unproductive aquatic ecosystems, including lakes, in the compilation by Duarte and Agusti (1998). CO<sub>2</sub> supersaturation in the majority of numerous lake measurements (Cole and others 1994), in 23 of 25 tundra lakes (Kling and others 1991) and in boreal forest lakes (Dillon and Molot 1997; Jonsson and others 2003) also supports the predominance of negative NEP due to degradation of organic matter from land and from wetland plants along the lake shore, although inflow of CO<sub>2</sub> supersaturated water contributes to the CO<sub>2</sub> emission to the atmosphere. Experiments directly demonstrate that removal of leaf input to forest ponds reduces  $R_{\text{COM}}$  and makes NEP less negative (Rubbo and others 2006). Moreover, experimental addition of inorganic <sup>13</sup>C to entire lakes and subsequent measurements of δ<sup>13</sup>C in different pelagic organic pools confirm the relatively greater support by terrestrially derived organic carbon to planktonic consumers as lake size and trophic decrease and dissolved organic color increases (Pace and others 2007). The 19 small lakes included in our analysis all have a close contact to land and a substantial input of both airborne and waterborne terrestrial organic matter that can support respiratory processes in the lakes. We confirm that negative NEP-values are a widespread feature over gradients in trophic status and land cover of small Danish lakes, including very eutrophic ones.

Organic matter dissolved in the water flowing to forest lakes in our study region showed a mean degradability of 1.5 mmol C l<sup>-1</sup> over 10 months (Sand-Jensen, unpublished) which would give rise to annual CO<sub>2</sub> emission rates from the lakes of 0.75–3.0 mol m<sup>-2</sup> for typical water retention times of 0.5–2 years (Algesten and others 2003). Degradable particulate organic matter of about one-third this magnitude may be carried by surface flow (Sand-Jensen and Pedersen 2005). Annual airborne leaf input from deciduous forest vegetation typically amounts to 250–500 g C per m along the lake shore (Fisher and Likens 1973) corresponding to 0.4–2.7 mol C m<sup>-2</sup> for our main range

of lake sizes (0.3–3.1 ha). This yields a maximum annual input of organic carbon available for degradation of about  $7 \text{ mol m}^{-2}$  which is of the same order of magnitude as our estimate of mean NEP in forest lakes ( $-10.1 \text{ mol O}_2 \text{ m}^{-2}$ ) and the estimates of annual  $\text{CO}_2$ -emission rates from tundra lakes (avg.  $7.7 \text{ mol m}^{-2}$ , Kling and others 1991), Scandinavian boreal lakes (avg.  $5.3 \text{ mol m}^{-2}$ , Jonsson and others 2007), and forest lakes in mid-Sweden ( $3.5\text{--}4.9 \text{ mol m}^{-2}$  in catchments 19–21, Algesten and others 2003). In contrast, our estimates of  $\text{CO}_2$  emission rates are much higher.

### Gas Fluxes and Excessive $\text{CO}_2$ Emission

We estimated much greater molar rates of  $\text{CO}_2$ -emission than  $\text{O}_2$ -uptake in our lakes. The regression slope between  $\text{CO}_2$  emission and  $\text{O}_2$  uptake was 2.4. If aerobic degradation of exogenous organic matter in the lakes is the main source of this  $\text{CO}_2$  emission and  $\text{O}_2$  uptake we should expect a molar ratio of  $\text{CO}_2/\text{O}_2$  close to 1.0. Anaerobic sediment respiration by use of alternative electron acceptors (nitrate, sulfate, and oxidized iron and manganese) and input of supersaturated groundwater would support greater molar release of  $\text{CO}_2$  than uptake of  $\text{O}_2$  (Torgersen and Branco 2007). Anaerobic sediment processes in a small, shallow, and rapidly flushed Connecticut pond (for example, denitrification and fermentation) have been invoked to explain the imbalance between the much greater annual release of 29.2 and  $30.3 \text{ mol CO}_2 \text{ m}^{-2}$  from the pond surface to the atmosphere in 2 years than the uptake of only  $2.7 \text{ mol O}_2 \text{ m}^{-2}$  in 1 year and release of  $9.1 \text{ mol O}_2 \text{ m}^{-2}$  in the other year (Torgersen and Branco 2008). We find it more likely for our small Danish lakes that the high  $\text{CO}_2/\text{O}_2$  ratio and the high emission rate of  $\text{CO}_2$  hide an error in the  $\text{CO}_2$ -emission estimate because the estimated inputs of groundwater  $\text{CO}_2$ , the internal  $\text{CO}_2$  release by loss of alkalinity, and the degradation of external input of organic matter, approximately matching  $\text{O}_2$  uptake from the atmosphere, are not sufficiently large to account for the  $\text{CO}_2$ -emission estimate. Groundwater in the region is greatly supersaturated with free  $\text{CO}_2$  (400–1000  $\mu\text{M}$ , Sand-Jensen and others 1995) which corresponds to annual emissions of  $0.2\text{--}2 \text{ mol CO}_2 \text{ m}^{-2}$  of lake surface at typical water retention times of 0.5–2 years which is too low to account for the high estimates of  $\text{CO}_2$  emission rates, though it will contribute to  $\text{CO}_2/\text{O}_2$  exchange ratios with the atmosphere above 1.0 (Figure 5). An additional  $\text{CO}_2$  source is loss of alkalinity by precipitation and permanent burial of  $\text{CaCO}_3$  and silicate minerals in the lake sediments

(McConnaughey and others 1994). Permanent sedimentation of  $\text{CaCO}_3$  is low, however, in these predominantly  $\text{CO}_2$  supersaturated lakes.

Accordingly, our  $\text{CO}_2$  emission rates are perhaps overestimated because piston velocities or  $\text{CO}_2$  gradients from water to air are overestimated or both. Piston velocities for  $\text{O}_2$  and  $\text{CO}_2$  used here resembled each other (Liss and Merlivat 1986), but direct comparisons are needed for small, wind sheltered lakes where organic surface layers can be prominent (Frew and others 2004).  $\text{CO}_2$  gradients across the water–air interface are overestimated if pre-noon  $\text{CO}_2$  concentrations in the water exceed daily averages and if  $\text{CO}_2$  in the stagnant air film exceeds standard atmospheric concentrations. No  $\text{CO}_2$  measurements are available for air films, but values of 150–200% saturation have been measured 1 m above the water surface of  $\text{CO}_2$  supersaturated streams on 5 calm mornings, whereas values close to 100% saturation were recorded on 13 mornings with more wind (Christensen 2000). Future continuous measurements of  $\text{CO}_2$  and  $\text{O}_2$  in lake water and atmospheric air and direct measurements of piston velocity are needed to improve measurements of whole-lake metabolism and evaluate potential errors in gas exchange rates with the atmosphere.

In conclusion, our results demonstrate that the small Danish lakes are systematically net heterotrophic, that even very eutrophic lakes remain net heterotrophic and that  $\text{O}_2$  uptake corresponds to the negative net ecosystem productivity probably driven by input of organic matter from land. Although  $\text{CO}_2$  input from groundwater and surface flow, internal  $\text{CO}_2$  generation by anaerobic respiration and precipitation of minerals support higher  $\text{CO}_2$  emission than  $\text{O}_2$  uptake, the presented  $\text{CO}_2$  emission rates are probably overestimated and deserve future attention.

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