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Carbon Cycling in Northern Temperate Lakes

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Carbon Cycling in Northern Temperate Lakes

Kristal D. Dubois

A thesis submitted to the Faculty of Graduate and Postdoctoral Studies
In partial fulfillment of the requirements for the degree of Ph.D. in Earth Sciences

Ottawa-Carleton Geoscience Centre
Department of Earth Sciences
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Legend

A ..... atmospheric flux
AGP ..... areal gross productivity
alk ..... alkalinity
AR ..... areal respiration
Chl-*a* ..... concentration of chlorophyll-*a*
CO_{2sat} ..... concentration of carbon dioxide at equilibrium
Cond ..... conductivity
$\delta^{13}C$ method ..... to measure GPP and R from C and O isotopes and concentrations
$\delta^{13}C_A$ ..... isotopic signature of carbon dioxide fluxing to or from the atmosphere
$\delta^{13}C_{ATM}$ ..... isotopic signature of atmospheric carbon dioxide
$\delta^{13}C_{CO2}$ ..... isotopic signature of dissolved carbon dioxide
$\delta^{13}C_{DIC}$ ..... isotopic signature of dissolved inorganic carbon
$\delta^{13}C_{DOC}$ ..... isotopic signature of dissolved organic carbon
$\delta^{13}C_{GW}$ ..... isotopic signature of inorganic carbon in groundwater
$\delta^{13}C_{obs}$ ..... measured isotopic composition of DIC
$\delta^{13}C_{pred}$ ..... isotopic composition of DIC as predicted by model
$\delta^{13}C_P$ ..... isotopic signature of photosynthesized carbon
$\delta^{13}C_R$ ..... isotopic signature of respired carbon
$\delta^{18}O$ method ..... to measure GPP from DO, O isotopes and R
$\delta^{18}O_A$ ..... isotopic signature of oxygen fluxing to or from the atmosphere
$\delta^{18}O_{ATM}$ ..... isotopic signature of atmospheric oxygen
$\delta^{18}O_{DO}$ ..... isotopic signature of dissolved oxygen
$\delta^{18}O_P$ ..... isotopic signature of photosynthesized oxygen
$\delta^{18}O_R$ ..... isotopic signature of respired oxygen
$\delta^{18}O_w$ ..... isotopic signature of oxygen in water
DIC ..... dissolved inorganic carbon
[DIC]gw ..... concentration of dissolved inorganic carbon in groundwater
DO ..... dissolved oxygen
DOC ..... dissolved organic carbon
DR ..... drainage ratio
ε_a ..... oxygen isotopic fractionation due to atmospheric flux
ε_g ..... oxygen isotopic fractionation due to gas transfer
ε_p ..... oxygen isotopic fractionation due to photosynthesis
ε_r ..... oxygen isotopic fractionation due to respiration
ε_s ..... oxygen isotopic fractionation due to dissolution
$\varepsilon_{a(CO2)}$ ..... carbon isotopic fractionation due to atmospheric flux
$\varepsilon_{aq\text{-}g}$ ..... carbon isotopic fractionation due to gas dissolution
ε_k ..... carbon isotopic fractionation due to gas transfer
$\varepsilon_{P(CO2)}$ ..... carbon isotopic fractionation due to photosynthesis
$\varepsilon_{r(CO2)}$ ..... carbon isotopic fractionation due to respiration

ε_{par} ..... light extinction coefficient
GPP ..... gross primary productivity
GPP:R ..... ratio of gross primary productivity to respiration
GPP-R ..... difference between gross primary productivity and respiration
K ..... gas transfer velocity
LA ..... lake surface area
O_{2sat} ..... concentration of dissolved oxygen at equilibrium
PAR ..... photosynthetically available radiation
R ..... respiration
SD ..... standard deviation
SE ..... standard error
T ..... temperature
TN ..... total nitrogen
TP ..... total phosphorous
VGP ..... volumetric gross productivity
VR ..... volumetric respiration
WA ..... watershed area
Z ..... depth of the mixed layer
zm ..... mean depth of lake

Abstract

We present two novel stable isotope methods for measuring lake metabolism and compare the results to traditional techniques. The $\delta^{18}O$ method measures planktonic gross primary production (GPP) from dissolved oxygen concentrations, isotopes and respiration (R) and the $\delta^{13}C$ method measures "whole-lake" GPP and R from dissolved oxygen and carbon concentrations and isotopes. All three methods showed GPP was greater than R over the ice-free season and estimates of GPP were not significantly different. There was also no significant difference in R as measured by bottle incubations and the $\delta^{13}C$ method However, the $\delta^{13}C$ method does not account for inputs of external carbon which will result in underestimation of R and overestimation of GPP. In systems with significant allochthonous carbon inputs, the $\delta^{13}C$ method cannot be accurate unless these inputs are accounted for.

The $\delta^{18}O$ method was used to measure metabolic parameters of twenty-one northern temperate lakes and showed GPP dominated over R during the ice-free season. GPP and R were most strongly correlated with lake temperature, which in turn is a function of the amount of solar radiation received by the lake. Our results imply that it is this solar radiation that drives planktonic gross primary productivity, which in turn drives the majority of planktonic respiration. Variation in dissolved organic carbon only explained 8% of the variation in planktonic R, while variation in planktonic GPP explained approximately 80% of the variation in planktonic R.

Despite general autotrophy in the lakes, they were generally oversaturated in CO_2 during the ice-free season, on average 252±25%. However, we found little evidence to conclude that this was the result of an excess of in situ respiration over production. The magnitude of the annual excess of R over GPP was not sufficient to account for the flux to

the atmosphere. Moreover, carbon evasion was not a function of respiratory flux, nor did the isotopic signature of dissolved CO_2 in the lakes present evidence of respiration. Groundwater inputs of carbon dioxide represent a plausible source for carbon dioxide oversaturation in some but not all of the lakes sampled.

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General Introduction

Carbon that cycles through a lake can originate from terrestrial, aquatic or atmospheric sources (Figure 1). One atom of carbon can be recycled within the lake hundreds of times through the processes of production and respiration or it can invade from the atmosphere and evade again within seconds. Organic or inorganic carbon can be introduced into a lake by groundwater or surface flow. Photoxidation can convert organic carbon into inorganic carbon. Organic carbon can be permanently buried within lake sediments or oxidized and mixed back into the water column. With this array of possibilities it is not surprising that the processes that control carbon cycling in aquatic systems are not well quantified.

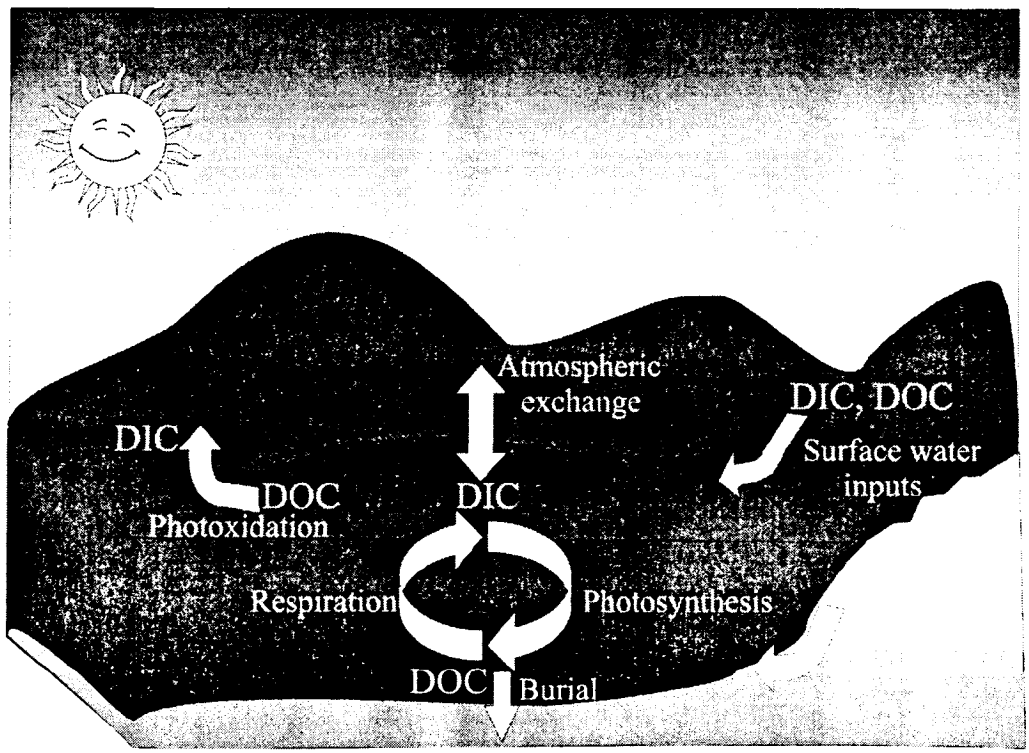

Figure 1. Major processes that influence dissolved organic carbon (DOC) and dissolved inorganic carbon (DIC) concentrations in lakes.

The balance between production and respiration is not only an important component of carbon dynamics in aquatic systems but also lies at the basis of our understanding of food web dynamics. If production exceeds respiration, a lake will be net autotrophic and the organic carbon which feeds higher trophic levels originates primarily *in situ*. Conversely, if respiration is greater than production, the lake will be net heterotrophic and the energy for the lake's food web must be supplemented by allochthonous sources.

Yet, the relative importance of primary productivity over community respiration has been a highly debated subject for many years. Some studies have found that lakes are net heterotrophic, that allochthonous carbon fuels a large part of bacterial metabolism and that the magnitude of net heterotrophy increases in unproductive aquatic ecosystem. As a result, lakes are net sources of CO_2 (del Giorgio et al. 1994; del Giorgio et al. 1997; Duarte and Agustí 1998). This net heterotrophy hypothesis is further supported by indirect evidence that bacteria can metabolize some allochthonous organic carbon input from a lake's watershed and that lakes are commonly supersaturated in carbon dioxide. Other ecologists have considered aquatic systems to be fuelled primarily by planktonic photosynthesis and have shown that even oligotrophic waters can be net autotrophic (Williams 1998; Carignan et al. 2000; Karl et al. 2003).

The metabolic balance debate is further confounded by widely varying results in a narrow geographic region. Studies done in the Eastern Townships region of Québec found that respiration exceeds photosynthesis in all but the most eutrophic ecosystems (del Giorgio and Peters 1994; Prairie et al. 2002). Carignan et al. (2000) found production to be greater than respiration in oligotrophic systems and allochthonous carbon metabolism to be an insignificant source of CO_2 in twelve lakes in the Laurentian region of Québec. Meech Lake,

north of Gatineau, Québec was found to be strongly production dominated in early-summer and strongly respiration dominated throughout the rest of the year (Wang and Veizer, 2000, 2004). The reason for the difference in these findings is unclear. It has been proposed that the differences in methodology are at the base of the differences in findings (Carignan et al. 2000). It is also possible that the lakes, although geographically within a 200 km radius, are limnologically different, causing differences in their metabolic balance.

Recent studies, on northern temperate lakes in both Europe and North America, have focused on the role of allochthonous carbon in lake metabolism (Prairie et al. 2002, Hanson et al. 2003, Jansson et al. 2000). Dissolved organic carbon in a lake system may act to increase the rate of respiration by providing an energetic subsidy and suppress production by absorbing incoming radiation, so that production is expected to exceed respiration at low levels of DOC and respiration is expected to exceed production at higher concentrations of DOC. The DOC threshold driving net autotrophy or net heterotrophy remains uncertain. Prairie et al. (2002) found levels of DOC above 6 mg L^{-1} lead to net heterotrophy while others (Hanson et al. 2003, Jansson et al. 2000) found lakes were net autotrophic with DOC levels up to 10 mg L^{-1}.

Despite advances in our understanding of the importance of dissolved organic carbon, the reason for the discrepancy between results of previous studies remains unclear. Are methodological differences underlying the difference? Are differences in the limnological characteristics of the lakes studies sufficient to explain the differences in metabolism? To elucidate the reason for differences in metabolic balance results of previous studies and to determine the source of carbon dioxide oversaturation we undertook a study of twenty-one lakes in three regions of Quebec using the isotope method of metabolic measurements.

Stables isotopes of dissolved oxygen can be used to determine the metabolic balance of aquatic systems (Quay et al. 1995; Luz et al. 2000). However, this methodology has not been rigorously compared to traditional methods of metabolic measurements. In Chapter 1 we propose two models to determine the balance of production and respiration in an aquatic system using stable isotopes. The first model uses stable isotopes of oxygen, the degree of oxygen saturation and bottle incubation measurements of respiration to measure gross primary production. However, because bottle incubations are used to measure respiration, this model does not completely take into account benthic or littoral processes and thus is most applicable as a measure of pelagic metabolic processes. The second model uses stable isotopes of both carbon and oxygen and the degree of carbon and oxygen saturation to estimate both gross primary production and respiration. It is not constrained by bottle incubations to measure respiration and thus takes into account benthic and littoral metabolic processes as well as integrates samples over the residence time of oxygen and carbon dioxide in the system. To test these models we sampled two lakes on a weekly basis over a year using both the traditional bottle method of metabolic measurements and the stable isotope methods.

The second chapter of this thesis uses these stable isotope models to determine the metabolic balance of twenty-one lakes in three regions of Quebec and to examine underlying causes in the differences in metabolism. Differences in morphometry and physiochemical parameters, in particular DOC, are used to examine differences in metabolism between lakes, and measures of production and respiration are compared with previous studies.

Whether lakes are seen as net autotrophic or heterotrophic, they are in general oversaturated in carbon dioxide. Cole et. al. (1994) surveyed 1835 lakes worldwide and found 87% were oversaturated in CO_2. Sobek et al. (2005) found that ninety-three percent of

4902 globally distributed lakes were oversaturated with carbon dioxide. While it is frequently presumed that net heterotrophy is the source of the carbon dioxide oversaturation, this has not been well documented.

Because dissolved carbon dioxide concentrations reflect benthic, littoral and pelagic processes, pCO_2 is heralded as an integrated, whole-lake, method of measuring production and respiration in aquatic systems. For the same reasons, carbon dioxide oversaturation is frequently presented as evidence of net heterotrophy in aquatic systems. However, if the source of CO_2 oversaturation is from external processes, a simple measure of pCO_2 cannot be used as a proxy for measuring rates of production and respiration in lakes, nor can oversaturation be considered an indication of net heterotrophy.

The role of northern forest biomes in the global carbon cycle has been a subject of intense debate for the last ten years since a study by Ciais et al. (1995) proposed the existence of a large terrestrial biospheric sink of CO_2 in the temperate latitudes of the Northern Hemisphere. Forest inventory data from temperate and boreal biomes suggests that about half of the "missing carbon sink" is in these forests (Liski et al. 2003). However, such inventories do not take into account the transport of carbon from forests to aquatic systems. If the source of carbon dioxide oversaturation in lakes is from forest ecosystems, then these models overestimate the magnitude of the proposed sink.

The third chapter of this thesis examines carbon dynamics in 23 Quebec lakes to determine the magnitude of carbon flux to the atmosphere from these lakes and to examine the underlying cause for carbon dioxide oversaturation. Two lakes were sampled on a weekly basis over one year to assess temporal changes and twenty-one lakes in three regions were sampled during the ice-free season to quantify differences in carbon dynamics between lakes. The magnitude of atmospheric flux, gross primary production (GPP) and community

respiration (R) were measured, as well as the isotopic composition of dissolved carbon. Benthic, as well as pelagic, net ecosystem productivity (NEP) was estimated to give a whole-lake account of carbon cycling. This estimate of NEP was compared with the annual atmospheric flux to determine if an excess of respiration was sufficient to account for the flux of CO_2 to the atmosphere. An isotopic mass balance model (Bade et al. 2004) was used in an attempt to determine if groundwater or surface water inputs were a plausible source of carbon dioxide oversaturation in the lakes.

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Chapter 1 The production – respiration balance of unproductive shield lakes: comparing estimates of GPP and R from stable isotopes with traditional bottle incubation techniques

Abstract

The isotopic composition of dissolved oxygen has previously been used to determine gross primary production (GPP) and respiration (R) in aquatic ecosystems, but this methodology has not been compared to conventional metabolic measurements. Here, we present two methods to measure metabolism from stable isotopes. The $\delta^{18}O$ method measures planktonic GPP from dissolved oxygen concentrations, isotopes and R. The $\delta^{13}C$ method measures GPP and R in the whole aquatic system from dissolved oxygen and carbon concentrations and isotopes. Estimates of GPP, R and GPP:R obtained with these methods in one oligotrophic and one mesotrophic lake are compared to conventional bottle measurements. All three methods showed GPP was greater than R over the ice-free season. Average GPP over the ice-free season as measured by the $\delta^{18}O$ method (177 ± 21 mg C m^{-3} d^{-1} in Lac Croche, 356 ± 27 mg C m^{-3} d^{-1} in Lac à l'Ours) from bottle incubations (188 ± 16 mg C m^{-3} d^{-1} in Lac Croche, 357 ± 41 mg C m^{-3} d^{-1} in Lac à l'Ours) and from the $\delta^{13}C$ method (196 ± 23 mg C m^{-3} d^{-1} in Lac Croche, 255 ± 30 mg C m^{-3} d^{-1} in Lac à l'Ours) were not significantly different. There was also no significant difference in R as measured by bottle incubations (122 ± 19 mg O_2 m^{-3} d^{-1} in Lac Croche and 252 ± 22 mg O_2 m^{-3} d^{-1} in Lac à l'Ours) and the $\delta^{13}C$ method (96 ± 23 mg O_2 m^{-3} d^{-1} in Lac Croche and 119 ± 30 mg O_2 m^{-3} d^{-1} in Lac à l'Ours). However, the $\delta^{13}C$ method does not account for inputs of external carbon which will result in underestimation of R and overestimation of GPP. In systems with significant allochthonous carbon inputs, the $\delta^{13}C$ method cannot be accurate unless these inputs are accounted for. All statistical tests and confidence intervals are reported at the α=0.05 critical level

Introduction

Measuring the balance between production, P, and respiration, R, is fundamental to our understanding of carbon flow and food web dynamics in aquatic systems. Yet, the relative importance of primary production over community respiration in marine and freshwater ecosystems has been highly debated for many years. Some researchers have found that external organic carbon supports baseline metabolism and that epilimnetic respiration exceeds photosynthesis in all but the most eutrophic ecosystems (e.g. del Giorgio and Peters 1993, 1994) while others (Carignan et al. 2000) found the epilimion of oligotrophic shield lakes to be net-autotrophic.

Conventional methods for estimating production in aquatic systems involve incubating samples and measuring the uptake of ^{14}C or the change in oxygen concentration. These methods can be labour intensive and require large incubators that are not often accessible. Also, because they incubate pelagic samples, they do not give a whole-ecosystem estimate of production and respiration, as benthic and littoral components are not included. Several methods involving stable isotopes of oxygen have also been used to estimate P in aquatic ecosystems. Bender and Grande (1987) proposed a model to determine the ratio of P to R from the isotopic composition of dissolved oxygen, $\delta^{18}O_{DO}$, and the degree of oxygen saturation, but their model does not include flux of O_2 to or from the atmosphere. Quay et al. (1995) expanded on this model and included an atmospheric component, but their model is mathematically undefined when the aquatic system is at 100% oxygen saturation or when $\delta^{18}O_{DO}$ is equal to the isotopic composition of oxygen in the atmosphere. Wang and Veizer (2000, 2004) showed that $\delta^{18}O_{DO}$ can be combined with measures of the isotopic composition of CO_2 to examine, in a non-quantitative fashion, the balance between P and R.

Luz and Barkan (2000) proposed a method to measure oceanic productivity with the triple isotopic composition of dissolved oxygen.

All of these methods are based on the isotopic fractionations that occur in the aquatic system. The isotopic composition of dissolved oxygen (DO) in an aquatic ecosystem is the result of three major processes: photosynthesis, respiration and exchange with the atmosphere. Dissolved atmospheric oxygen has a $\delta^{18}O$ of 24.2‰ (vs. VSMOW; Figure 1-1) (Benson and Krause 1984). Because aquatic photosynthesis is a non-fractionating process (Guy et al. 1993), DO produced by photosynthesis ($\delta^{18}O_P$) has the same isotopic value as the oxygen atoms in the water molecules from which it is produced. In our study area, the $\delta^{18}O$ of water ($\delta^{18}O_W$) is about -10‰, so photosynthesis produces DO with a light isotopic composition. During respiration, the uptake of the light isotope of oxygen is approximately 20‰ greater than uptake of the heavy isotope of oxygen and thus respiration enriches the dissolved oxygen pool in the heavy isotope (Kiddon et al. 1993).

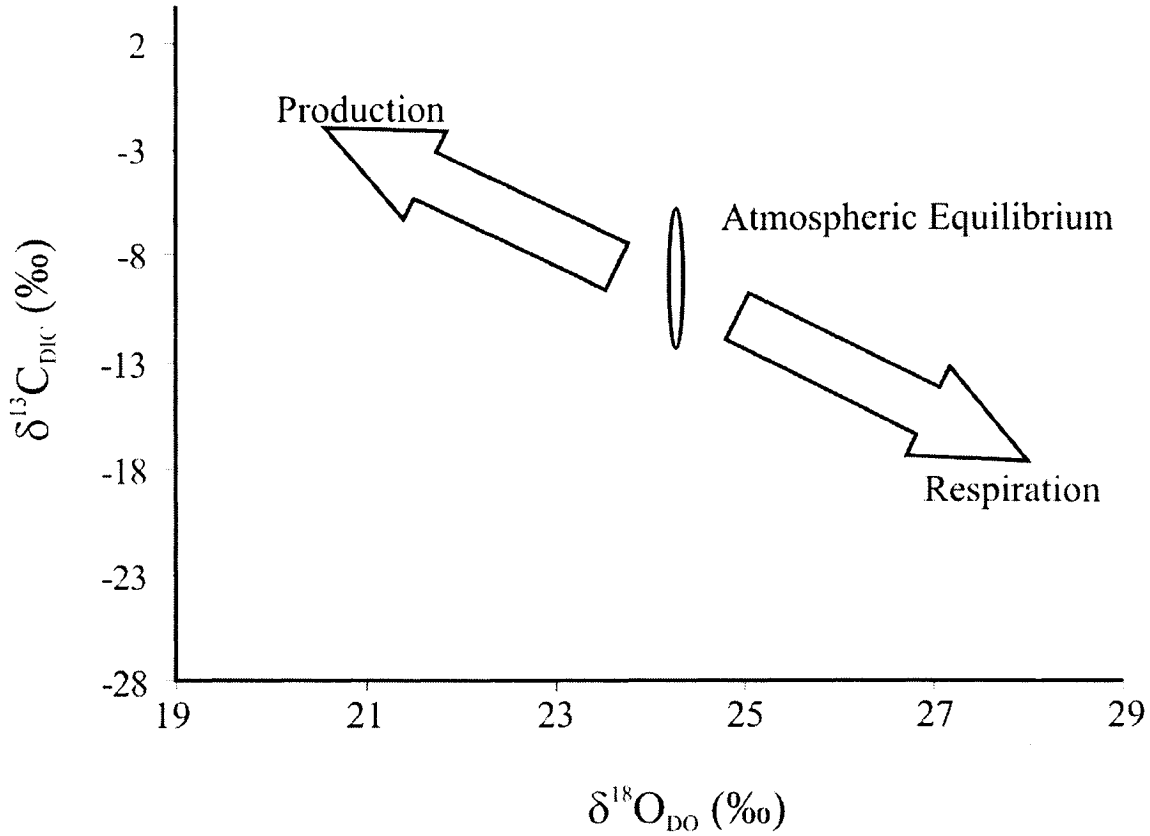

Figure 1-1. Effect of production, respiration and atmospheric exchange on the isotopic composition of dissolved oxygen, $\delta^{18}O_{DO}$ and dissolved inorganic carbon, $\delta^{13}C_{DIC}$.

The isotopic composition of dissolved inorganic carbon, $\delta^{13}C_{DIC}$, is also indicative of metabolic processes. Atmospheric carbon dioxide has an isotopic composition of about –8.5‰ and dissolution of this CO_2 into water causes fractionation as the carbon speciates, so that the $\delta^{13}C_{DIC}$ that originates as atmospheric CO_2 has a pH- and temperature-dependent isotopic composition ranging between –5.5 and –11.8 ‰ in our study lakes (Figure 1-1). Aquatic photosynthesis preferentially consumes the light carbon isotope of dissolved CO_2, leaving the carbon dioxide pool enriched in ^{13}C (Baird et al. 2001) to varying degrees, depending on the degree of carbon dioxide limitation. The organic matter produced in

aquatic photosynthesis is depleted in ^{13}C, with a $\delta^{13}C$ value about 20‰ less than $\delta^{13}C_{CO2}$. In situ respiration consumes this ^{13}C depleted organic matter and produces CO_2 with a similarly depleted isotopic signature (Keough et al. 1998).

Stable isotope methods of estimating production and respiration have never been directly compared to conventional metabolic measurements. Here we outline two methods of estimating metabolic parameters from stable isotopes. The $\delta^{18}O$ method estimates gross primary production (GPP) from the isotopic composition of dissolved oxygen, the isotopic composition of water and the concentration of dissolved oxygen, but is dependent on bottle incubation estimates of respiration. The $\delta^{13}C$ method estimates GPP and R from stable isotopes of dissolved oxygen and inorganic carbon and the concentrations of dissolved oxygen and inorganic carbon and is not dependent on bottle incubations. We compare the estimates of GPP and R and the metabolic balance, GPP:R, obtained from these two methods in one oligotrophic and one mesotrophic lake with bottle incubations methods.

Materials and Procedures

Study Site –

Both lakes are located on the Canadian Shield, approximately 60 km northwest of Montreal, Quebec, Canada. The area is underlain by anorthositic bedrock covered by 1-5m of glacial till. Soils are mostly Humic Cryorthods (US classification) or Orthic Ferro-Humic Podzols (Canadian classification). Catchments are forested (> 95%) primarily with sugar maple (*Acer saccharum*), yellow birch (*Betula alleghaniensis*), beech (*Fagus grandifolia*) and poplar (*Populus tremuloïdes*). Annual precipitation averages 1100 mm y^{-1}, with 30% falling as snow. Lac Croche is a small (0.19 km^2), pristine oligotrophic clearwater lake with a mean depth of 5.1 m in a watershed of 0.88 km^2. Alkalinity is low in Lac Croche (annual

average of 82 meq m^{-3}) and pH is slightly below neutral (6.1–6.9). Total phosphorous (TP), total nitrogen (TN) and dissolved organic carbon (DOC) concentrations are 3.8 mg m^{-3}, 211 mg m^{-3} and 3520 mg m^{-3}, respectively (Carignan et al. 1998). Macrophytes are virtually absent in Lac Croche, but epilithic and epipelic communities are well-developped. Total P and DOC are higher (14 mg m^{-3} and 6.64 g m^{-3}) in Lac à l'Ours due to its larger drainage ratio and to the presence of wetlands in its watershed. Average alkalinity and pH are 310 meq m^{-3} and 6.2, respectively. Lac à l'Ours has an area of 0.15 km^2, a watershed of 3.26 km^2 and a mean depth of 6.7 m. Twenty-two cottages have been built on its shores.

Sampling –

Chemical and physical parameters of both lakes were measured on a weekly basis between May 2002 and March 2003. Epilimnetic production was measured twice monthly during the ice-free season from bottle incubations. Community respiration was measured twice monthly during the entire sampling period. Water was collected with a 4-liter Van Dorn Bottle between 07h00 and 10h00. Morning sampling ensured that the epilimnion was completely mixed during the summer stratification period. Throughout this report, the epilimnion is defined as the surface mixed layer where the vertical temperature gradient does not exceed 1°C m^{-1} in the morning. Water samples for respiration and production measurements were taken from the entire epilimnetic water column and pooled in 20 L dark polyethylene containers. Water for isotopic analysis was collected on a weekly basis from mid-epilimnion in 40 mL amber glass bottles with silicon/teflon septa for the isotopic composition of oxygen in water, $\delta^{18}O_w$, the isotopic composition of dissolved inorganic carbon, $\delta^{13}C_{DIC}$, and the isotopic composition of dissolved organic carbon, $\delta^{13}C_{DOC}$. Rubber septa were utilized for water samples used for measurement of the isotopic composition of

dissolved oxygen, $\delta^{18}O_{DO}$. All samples were poisoned with $HgCl_2$ to approximately 150 ppm and refrigerated at 4°C before analysis (within 4 months).

Physical and Chemical Analyses –

Oxygen and temperature profiles were measured at half-meter intervals with a YSI Model 55 instrument, equipped with a stirrer. The probe was calibrated prior to each use in vapour-saturated air with respect to atmospheric pressure, within 2 °C of epilimnetic temperature. The degree of oxygen saturation was calculated with respect to temperature and local barometric pressure according to Benson and Krause (1984). Chlorophyll concentration was measured (Sartorg and Grobbelaar 1984) on a biweekly basis by spectrophotometery after overnight extraction of frozen GF/C filters in cold ethanol and corrected for phaeopigments. Photosynthetically available radiation (PAR) was measured with a Li-Cor 190 sensor and the PAR extinction coefficient of the water column was measured (Li-Cor LI-192 sensor) twice monthly at half-meter intervals. Carbon dioxide concentrations were measured at one-meter intervals throughout the water column. Samples were taken in 60 mL syringes, transported to the lab and their temperature allowed to equilibrate with cool water. Thirty ml of sample was equilibrated with 30 mL CO_2 free gas and the carbon dioxide concentration of the resultant gas measured with a LI-COR LI-820 CO_2 analyser. Henry's law was then used to calculate the concentration of dissolved CO_2 in the water samples.

Bottle incubations-

Water used for metabolic rate measurements was distributed in clear and dark 300 mL pyrex bottles that were placed in a light gradient incubator, equipped with a Phillips MH1000, 1,000 W metal-halide lamp. It provided six irradiance levels ranging from

approximately 30 to 1000 μE m^{-2} s^{-1} and three replicate bottles were incubated at each level. These levels were quantified during the incubation using a Biospherical QSL-101 4-pi quantum meter freshly calibrated by the manufacturer. Incubations were performed at in situ temperatures and lasted 4 hours for production measurements and between 6 and 8 hours for respiration measurements. A high-precision Winkler method (Carignan et al. 1998) was used to measure the net production of oxygen (NP) and community respiration (R) from changes in dissolved oxygen concentration in clear and dark bottles during the incubation. The detection limits for NP and R were 2.3 and 1.7 mg O_2 m^{-3} h^{-1} respectively. Daily volumetric (VR) and areal (AR) respiration rates were calculated assuming that respiration rates measured from water sampled in the morning were representative of the entire day. We assumed equal dark and light algal respiration and calculated gross production during the incubation as NP - R.

The GP vs PAR curves were then used to calculate photosynthetic parameters using the computer program PSPARMS (Fee 1998). The chlorophyll-dependent rate of photosynthesis at optimal PAR (P^B_m, mg O_2 mg Chl^{-1} h^{-1}), the chlorophyll dependent slope of the photosynthesis versus PAR curve at low irradiance levels (α^B, mg O_2 mg Chl^{-1} E^{-1} m^2) and the saturation PAR (I_k, E m^{-2} h^{-1}) were calculated at all dates for both lakes. To estimate the amount of photosynthesis during the entire stratification period, the computer program YTOTAL (Fee 1998) was used with the measured daily PAR value. The program uses chlorophyll concentrations, P^B_m and α^B (all linearly interpolated from the input data) and the fraction of solar PAR that reaches each depth to calculate the photosynthesis versus depth profile. Daily areal gross planktonic photosynthesis rates (AGP) were calculated from bottle incubation measurements and PAR data using the computer program YTOTAL (Fee 1998).

Oxygen isotopic analyses –

$\delta^{18}O_W$ was measured at the G.G. Hach Isotope Laboratory (University of Ottawa). One mL of sample was flushed with a gas mixture of 2% by volume CO_2, left to equilibrate overnight at 25°C and the resultant CO_2 was then analyzed on a triple collector VG SIRA 12 mass spectrometer, with a standard deviation of 0.1‰. The isotopic composition of dissolved oxygen was measured at the National Water Research Institute (Saskatoon, Saskatchewan) for the samples collected between May and August 2002, and at the G.G. Hach Isotope Laboratory for samples collected between September 2002 and March 2003. Samples were analyzed by creating a 5 mL helium headspace, equilibrating the water sample with the headspace and analyzing an aliquot of the resulting gas by continuous flow mass spectrometry using a Micromass Optima instrument (Wassenaar and Koehler 1999). The standard deviation was 0.17‰ for samples measured at the National Water Research Institute and 0.4‰ for samples measured at the G.G. Hach Isotope Laboratory. Throughout this report, the $^{18}O/^{16}O$ isotope ratios in water and dissolved oxygen are expressed in ‰ with:

$$\delta^{18}O = \left(\frac{(^{18}O/^{16}O)_{sample}}{(^{18}O/^{16}O)_{VSMOW}} - 1 \right) \times 1000 \qquad (1)$$

where VSMOW is the international Vienna Standard Mean Ocean Water.

Carbon Isotope Analyses –

Samples for $\delta^{13}C_{DIC}$ and $\delta^{13}C_{DOC}$ were analysed at the G. G. Hatch Isotope Laboratory on an OI Analytical "TIC-TOC" Analyser following the procedure outlined by St. Jean (2003). Briefly, samples were first analysed for the concentration of organic and inorganic carbon and then for isotopic composition of DIC and DOC by helium carrying the resulting CO_2 organic/inorganic from the TIC-TOC analyser into a Finnigan Mat DeltaPlus isotope ratio mass spectrometer for analysis by continuous flow. Standard deviation of isotopic samples was 0.2‰. The isotopic composition of dissolved carbon dioxide, $\delta^{13}C_{CO2}$,

was calculated from $\delta^{13}C_{DIC}$, pH and temperature using the fractionation equations of Zhang et al. (1995) and equations for temperature and pH dependent carbonate speciation (Drever 1997).

$\delta^{18}O$ method, calculating GPP from oxygen isotopes –

The dissolved oxygen mass balance in an aquatic system is controlled by production from photosynthesis, consumption due to respiration, and exchange with the atmosphere. Thus, the change in the concentration of oxygen, $[O_2]$, over time is equal to the rate of gross primary production, GPP, minus the rate of respiration, R, minus the oxygen that evades to the atmosphere:

$$\frac{d[O_2]}{dt} = GPP - R - \frac{K_{O_2}}{Z}(O_2 - O_{2sat}) \qquad (2),$$

where K_{O2} is the gas transfer velocity (m d^{-1}), Z is the depth of the mixed layer (m), O_{2sat} is the concentration of oxygen at equilibrium (mg O_2 m^{-3}), calculated from temperature and pressure (Benson and Krause 1984), and O_2 is the measured concentration of oxygen (mg O_2 m^{-3}).

The isotope mass balance for the system is:

$$\frac{d[O_2]^{18}O_{DO}}{dt} = GPP^{18}O_P - R^{18}O_R - \frac{K_{O_2}}{Z}\alpha_G(O_2{}^{18}O_{DO} - O_{2sat}{}^{18}O_A\alpha_s) \qquad (3).$$

where each term in (2) has been multiplied by its respective isotopic composition. $\delta^{18}O_P$ is the isotopic ratio of oxygen produced by photosynthesis and $^{18}O_R$ is the isotopic ratio of oxygen produced by respiration, $^{18}O_A$ is the isotopic ratio of atmospheric oxygen, α_G is kinetic gas transfer fractionation factor and α_s is the fractionation factor that results from the preferential solubility of ^{16}O. To simplify equation 3 we assume that the aquatic system is sufficiently large to smooth short duration variations of $^{18}O_{DO}$, $^{18}O_W$, R, K_{O2}, O_2 and α_s. By substituting equation 2 into equation 3, equation 3 can be solved for GPP (Appendix 1):

$$GPP = \frac{R({}^{18}O_{IX} - {}^{18}O_R) + \frac{K_{O_2}}{Z}(O_2 - O_{2sat}) - \frac{K_{O_2}}{Z}\alpha_G({O_2}^{18}O_{IX} - O_{2sat}{}^{18}O_{IX}\alpha_S)}{({}^{18}O_{IX} - {}^{18}O_P)} \quad (4).$$

To calculate GPP from equation 4, seven variables must be measured (summarized in Table 1-1). Respiration, R, was measured from dark bottle incubations by the procedure described above in units of mg O_2 m^{-3} d^{-1}. The oxygen isotope ratio of water, $^{18}O_W$, and dissolved oxygen, $^{18}O_{DO}$, were measured and input into equation 4 as the ratio of ^{18}O to ^{16}O. Depth of the mixed layer, temperature and pressure and the concentration of oxygen are required to measure the rate of atmospheric flux, A. Cole and Caraco (1998) used SF_6 to measure gas transfer velocity in a small oligotrophic lake. They found that the gas transfer velocity for a gas with a Schmidt number of 600, K_{600}, was independent of wind at low wind speeds and that it averaged 2.65 ± 0.12 cm h^{-1}. Conditions, like lake size and wind speed, in the lake studied by Cole and Caraco were similar to lakes Croche and à l'Ours. We converted the K_{600} obtained by Cole and Caraco to K_{O2} using the temperature-dependent Schmidt number of oxygen, Sc_{O2}, (Wanninkhof 1992) and the relationship:

$$K_{O_2} = K_{600}\left(\frac{Sc_{O_2}}{600}\right)^{-0.50} \quad (5).$$

Aquatic photosynthesis converts the oxygen in a water molecule into dissolved oxygen without fractionation so that the dissolved oxygen that comes from production has the same ^{18}O value as the source water $^{18}O_W$ (Guy et al. 1993). A respiration fractionation factor, α_r, of 0.982 (Quay et al. 1995) was used. The influx of oxygen from the atmosphere has an isotopic composition that is equal to the atmospheric value, 0.002052 or 23.5‰, multiplied by the ratio of gas transfer velocities of $^{18}O^{16}O$ to $^{16}O^{16}O$ (α_g, 0.9972, Knox et al. 1992) and the ratio of solubilities of $^{18}O^{16}O$ to $^{16}O^{16}O$ which is temperature dependent (α_s,

((-0.730+(427/T))÷1000)+1), Benson and Krause 1984). The isotopic composition oxygen evading to the atmosphere is equal to the value of dissolved oxygen, $^{18}O_{DO}$ multiplied by α_G.

Table 1-1. Factors used to calculate GPP from equation 4. Respiration (R, mg O_2 m^{-3} d^{-1}); atmospheric flux (A, mg O_2 m^{-3} d^{-1}); gas transfer velocity (K_{O2}, m d^{-1}); depth of the mixed layer (Z, m); concentration of oxygen at equilibrium (O_{2sat}, mg O_2 m^{-3}); measured concentration of oxygen (O_2, mg O_2 m^{-3}); temperature (°C); isotopic composition of dissolved oxygen, photosynthesized oxygen, water, respired oxygen and atmospheric oxygen ($^{18}O_{DO}$, $^{18}O_P$, $^{18}O_w$, $^{18}O_R$, $^{18}O_{ATM}$); fractionation due to respiration, gas transfer and solution (α_R, α_G, α_S).

Variable			Source	
R			Measured	
A	$\frac{K_{O_2}}{Z}(O_2 - O_{2sat})$			
		O_2, Z	Measured	
		O_{2sat}	calculated from temperature and pressure	Benson and Krause 1984
		K_{O2}	$0.636\left(\frac{1800.6-120.10(T)+3.7818(T^2)-0.047608(T^3)}{600}\right)^{0.50}$	Cole and Caraco 1998; Wanninkhof 1992
$^{18}O_{DO}$			Measured	
$^{18}O_P$	$^{18}O_W$			Guy et al. 1993
		$^{18}O_W$	Measured	
$^{18}O_R$	$^{18}O_{DO} \times \alpha_R$			
		$^{18}O_{DO}$	Measured	
		α_R	0.982	Quay et al. 1995
$^{18}O_A$		$\delta^{18}O_{ATM}$	0.002052 (23.5‰)	Kroopnick and Craig 1972
		α_G	0.9972	Knox et al. 1992
		α_S	$\left(\left(-0.730+\left(\frac{427}{T+273.15}\right)\right)\div 1000\right)+1$	Benson and Krause 1984

$\delta^{13}C$ method, calculating GPP and R from O and C isotopes –

Because the $\delta^{18}O$ method described above is based on bottle measurements of respiration, it does not completely include respiration that occurs in the littoral or benthic regions of the lake. Here, we propose a model for estimating GPP and R that does not rely on bottle incubations for respiration measurements. Like $\delta^{18}O_{DO}$, the isotopic composition of dissolved inorganic carbon, $\delta^{13}C_{DIC}$, is also influenced by respiration and production. An estimate for both GPP and R, which reflects pelagic, littoral and benthic respiration and production can be obtained by combining oxygen and carbon fluxes. The method described below uses the same oxygen isotope fluxes described previously and a simple model for carbon fluxes in the lake system, based solely on aerobic respiration, production and atmospheric carbon flux. The accuracy of this model would of course be improved if other presently unquantified components of the lake carbon cycle, such as methanogenesis, anaerobic respiration, external inputs of carbon dioxide and photooxidation were taken into account.

Like the dissolved oxygen mass balance in an aquatic system, the mass balance of DIC is controlled by consumption by photosynthesis, production by respiration, and exchange with the atmosphere. Following the model of Bade et al. (2004), we assume the change in the concentration of DIC over time is equal to the rate of respiration, R, minus the rate of gross primary production, GPP, minus the flux of CO_2 to the atmosphere, A_{CO2}.

$$\frac{dDIC}{dt} = R - GPP - \frac{K_{CO_2}}{Z}(CO_2 - CO_{2sat}) \qquad (6).$$

where, as for oxygen, K_{CO2} is the gas transfer velocity (m d^{-1}), Z is the depth of the mixed layer (m), CO_{2sat} is the concentration of carbon dioxide in equilibrium with the atmosphere (mmol CO_2 m^{-3}), and CO_2 is the measured concentration of carbon dioxide (mmol CO_2 m^{-3}).

We converted the K_{600} obtained by Cole and Caraco to K_{CO2} using the temperature-dependent Schmidt number of carbon dioxide, Sc_{O2}, (Wanninkhof 1992).

The isotope mass balance for the system is:

$$\frac{dDIC^{13}C_{DIC}}{dt} = R^{13}C_R - GPP^{13}C_P - \frac{K_{CO_2}}{Z}(CO_2{}^{13}C_{CO_2} - CO_{2sat}{}^{13}C_A) \quad (7)$$

where each term in (13) has been multiplied by its respective carbon isotopic composition in ‰ units. $^{13}C_{DIC}$ is the isotopic ratio of dissolved inorganic carbon, $^{13}C_R$ is the isotopic ratio of respired carbon, $\delta^{13}C_P$ is the isotopic ratio of carbon produced by photosynthesis, $\delta^{13}C_{CO2}$ is the isotopic ratio of dissolved CO_2 and $\delta^{13}C_A$ is the isotopic ratio of atmospheric carbon dioxide. To simplify equation 8 we assume that the aquatic system is sufficiently large to smooth short duration variations of $^{13}C_{DIC}$, $^{13}C_R$, $^{13}C_{CO2}$, GPP, K_{CO2}, CO_2 and CO_{2sat}.

By substituting equation 7 into equation 8, equation 8 can be solved for R (Appendix 1):

$$R = \frac{GPP(^{13}C_{DIC} - ^{13}C_P) + \frac{K_{CO_2}}{Z}(CO_2 - CO_{2sat}) - \frac{K_{CO_2}}{Z}(CO_2{}^{13}C_{CO_2} - CO_{2sat}{}^{13}C_A)}{(^{13}C_{DIC} - ^{13}C_R)} \quad (8)$$

Variables used in equation 8 are summarized in Table 1-2. Respiration produces dissolved CO_2 with the isotopic composition of dissolved organic carbon, $^{13}C_{DOC}$, measured in ‰ VPDB (Keough et al. 1998, but see assessment). The isotopic ratio of dissolved carbon dioxide, $^{13}C_{CO2}$, was calculated from $^{13}C_{DIC}$, pH, and temperature, following the isotopic speciation equations in Zhang et al. (1995). To calculate the isotopic ratio of photosynthesized carbon, $^{13}C_P$, we assume that production fractionates carbon by 20‰ relative to $\delta^{13}C_{CO2}$ (α_P=1.020, Laws et al. 1995). We use a fractionation factor below the maximum as it is unlikely that an assemblage of phytoplankton all are fractionating maximally due to differences in growth rate or carbon sources (Bade et al. 2004, Laws et al. 1995). The isotopic composition of invading atmospheric CO_2, $^{13}C_A$, is equal to the

atmospheric value multiplied by fractionation due to gas dissolution, $\alpha_{aq\text{-}g}$, and kinetic fractionation due to gas transfer α_K. The isotopic ratio of CO_2 evading to the atmosphere, $^{13}C_{CO2}$, is calculated from $^{13}C_{DIC}$, pH and temperature according to Zhang et al. and $\alpha_{aq\text{-}g}$.

Finally, equations 4 and 8 for GPP and R can be combined and solved simultaneously by itteration to provide estimates of GPP and R that are not limited by bottle incubations (Appendix 1).

Table 1-2. Factors used to calculate R and GPP from equations 4 and 8. Atmospheric flux (A, mmol CO_2 m^{-3} d^{-1}); gas transfer velocity (K_{CO2}, m d^{-1}); depth of the mixed layer (Z, m); concentration of carbon dioxide at equilibrium (CO_{2sat}, mmol CO_2 m^{-3}); measured concentration of carbon dioxide (CO_2, mmol CO_2 m^{-3}); temperature (°C); isotopic composition of photosynthesized carbon, dissolved carbon dioxide, dissolved inorganic carbon, respired carbon, dissolved organic carbon, dissolved atmospheric carbon and atmospheric carbon dioxide ($\delta^{13}C_P$, $\delta^{13}C_{CO2}$, $\delta^{13}C_{DIC}$, $\delta^{13}C_R$, $\delta^{13}C_{DOC}$, $\delta^{13}C_A$, $\delta^{13}C_{ATM}$ ‰), fractionation due to respiration, dissolution and kinetic fractionation during gas transfer (α_P, $\alpha_{aq\text{-}g}$, α_k).

Variable		Source		
A_{CO2}	$\frac{K_{CO_2}}{Z}(CO_2 - CO_{2sat})$			
		CO_2, Z	Measured	
		CO_{2sat}	calculated from temperature and pressure	
		K_{CO2}	$0.636\left(\frac{1911.1-118.11(T)+3.4527(T^2)-0.041320(T^3)}{600}\right)^{0.50}$	Cole and Caraco 1998; Wanninkhof 1992
$^{13}C_P$	$^{13}C_{CO2} \times \alpha_P$			
		$^{13}C_{CO2}$	Calculated from $\delta^{13}C_{DIC}$, temperature, pH and fractionation factors for carbon speciation	Zhang et al. 1995
		$^{13}C_{DIC}$	Measured	
		α_P	1.020	Bade et al. 2004; Laws et al. 1995
$^{13}C_R$	$^{13}O_{DOC}$			
		$\delta^{13}C_{DOC}$	Measured	
$^{13}C_A$	$\delta^{13}C_{ATM} \times \alpha_{aq\text{-}g} \times \alpha_k$		if net flux from the atmosphere	
		$\delta^{13}C_{ATM}$	-8.5 ‰	
		α_k	0.9992 at 21°C, 0.9991 at 5°C	Zhang et al. 1995
		$\alpha_{aq\text{-}g}$	((-0.0049 T(°C)-1.31) ÷ 1000) + 1	Zhang et al. 1995

Data analysis –

The precision of Winkler titrations and isotopic measurements are reported as ± one standard error (SE) of the mean of n determinations where $SE=SD/(n)^{1/2}$ and SD is the standard deviation. Addition and subtraction errors in the calculation of R, GPP and NPP were calculated as $SE_{A\pm B}=(SE^2_A+SE^2_B)^{1/2}$.

The confidence intervals of GPP from the $\delta^{18}O$ method were calculated by expanding the error of GPP from equation 4 in terms of a Taylor's Series as a function of the error of the variables R, (O_2-O_{2sat}), K, $\delta^{18}O_{DO}$, $\delta^{18}O_W$ and $\delta^{18}O_R$ (Kendall and Stuart 1977). The partial differentials of GPP in equation 4 with respect to R, O_2, O_{2sat}, $^{18}O_{DO}$, $^{18}O_P$ and $^{18}O_R$ were squared and multiplied by the variance associated with the variables. The variances of O_2, O_{2sat}, $^{18}O_{DO}$, $^{18}O_P$ and $^{18}O_R$ were 0.04 mg l^{-1}, 0.04 mg l^{-1}, 0.16‰, 0.01‰ and 0.16‰ respectively, while the variance of R was measured for each case. The standard error is then the square root of the sum of these products. The same procedure was followed to calculate confidence intervals of GPP and R from the $\delta^{13}C$ method, except the carbon variables were also included. The variances of CO_2, CO_{2sat}, $^{13}C_{DIC}$ and $^{13}C_{DOC}$, were 0.25 mg l^{-1}, 0.25 mg l^{-1}, 0.04‰ and 0.04‰, respectively. All statistical tests and confidence intervals are reported at the $\alpha=0.05$ critical level (Appendix 1).

Assessment

GPP and R from bottle incubations –

In Lac Croche volumetric epilimnetic respiration rates (VR) ranged from 16 to 244 mg O_2 m^{-3} d^{-1} with a weighted ice-free season mean of 122 ± 19 mg O_2 m^{-3} d^{-1}. In Lac à l'Ours, VR ranged from 57 to 406 mg O_2 m^{-3} d^{-1}, with a weighted mean of 252 ± 23 mg O_2 m^{-3} d^{-1} (Table 1-3). These respiration rates account for all process that consume O_2 in the bottles, but do not include photolytic processes that may consume or produce O_2.

Table 1-3. Physical and chemical properties of the water column and metabolic rates observed in Lac Croche and Lac à l'Ours from May to October, 2002. Temperature (°C); thickness of the mixed layer (Z, m); chlorophyll a (mg m^{-3}); light extinction coefficient (ε_{par}, m^{-1}); areal gross epilimnetic production, areal epilimnetic respiration (VGP and VR, mg O_2 m^{-3} d^{-1}) and metabolic balance (GPP:R) as measured from bottle incubations. Confidence intervals are at the α=0.05 critical level. Additional data can be found in Appendixes 2 and 3.

Lake	Date	T	Z	Chl a	ε_{par}	VGP	VR	GPP:R
Croche	23 May	10.0	3.25		0.58	110±60	70±32	1.6±0.57
	03 Jun	14.3	3.25	0.8	0.64	98±26		
	20 Jun	16.6	3.00	0.7	0.70	190±30	172±46	1.1±0.24
	01 Jul	24.2	2.50	1.2	0.60	331±22	244±24	1.4±0.12
	15 Jul	22.4	3.00	1.8	0.68	304±56	226±40	1.3±0.18
	29 Jul	21.3	3.50	1.9	0.69	316±116	201±28	1.6±0.31
	11 Aug	22.3	4.00	1.6	0.61	304±16	120±28	2.5±0.26
	23 Aug	21.6	4.00		0.62	257±22	95±52	2.7±0.63
	04 Sep	21.0	4.25	0.9	0.60	171±22	133±56	1.3±0.23
	17 Sep	18.4	4.75	1.2	0.59	142±48	41±52	3.4±1.69
	01 Oct	15.9	6.75	2.5	0.60	98±11	19±88	5.1±8.46
	23 Oct	8.3	8.00	1.9	0.69	49±8	16±92	3.0±5.89
à l'Ours	23 May	8.7	4.75		2.12	112±50	76±4	1.5±0.33
	04 Jun	15.4	2.75	3.8	1.25	436±158	295±48	1.5±0.31
	21 Jun	19.6	2.25	1.5		390±242	336±60	1.2±0.16
	03 Jul	27.4	2.25	4.5	1.52	569±42	406±80	1.4±0.21
	17 Jul	21.8	2.50	3.6	1.30	341±84	357±28	1.0±0.13
	31 Jul	24.0	2.75	4.2	1.37	699±240	241±40	2.9±0.30
	24 Aug	20.9	2.75		1.31	376±68	263±48	1.4±0.20
	04 Sep	20.9	3.00	3.1	1.30	422±32	256±72	1.7±0.27
	18 Sep	17.9	3.75	4.8	1.21	358±50	237±118	1.5±0.35
	02 Oct	16.1	4.00	4.5	1.24	224±52	148±92	1.5±0.44
	24 Oct	7.4	10.5	3.2	1.50	32±34	57±98	0.6±0.34

VGP ranged from 16 to 383 mg O_2 m^{-2} d^{-1} in Lac Croche and from 12 to 699 mg O_2 m^{-2} d^{-1} in Lac à l'Ours. Because sampling was not always conducted at even intervals, the time weighted average of VGP over the ice-free season was calculated: 188 ± 16 mg O_2 m^{-2} d^{-1} in Lac Croche and 357 ± 41 mg O_2 m^{-2} d^{-1} in Lac à l'Ours (Table 1-3). These values are similar to those previously published for these lakes by Carignan et al. (2000).

In Lac Croche, the ratio between GPP and R fluctuated around 1 in early summer and production became more dominant later in the summer. Both GPP and R declined in the fall, though R rates declined significantly more than GPP rates (Figure 1-2A). GPP:R over the ice-free season was calculated by determining total photosynthesis over the season, ΣGPP, from YTOTAL (Fee 1998) divided by total respiration over the season, ΣR. ΣR was estimated by linear interpolation between sampling dates. In Lac Croche the weighted average of GPP:R over the ice-free season was 1.8 ± 0.6. In Lac à l'Ours GPP:R fluctuated around unity in the spring and early summer. Production was, on average, more important than respiration during mid-summer. In late summer and fall, production declined more rapidly than respiration (Figure 1-2B). Over the ice-free season in Lac à l'Ours, ΣGPP/ΣR was 1.4 ± 0.3.

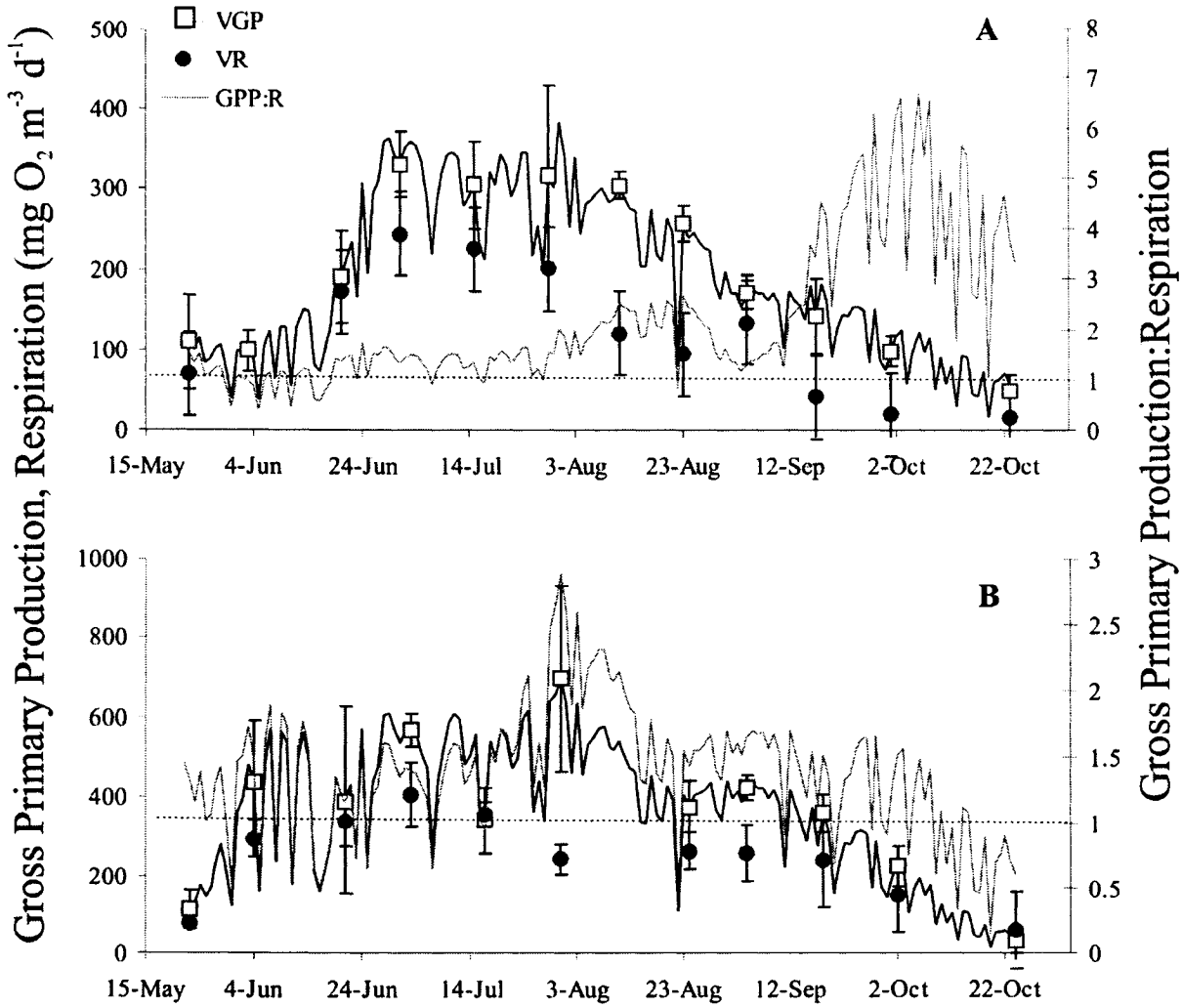

Figure 1-2.Volumetric gross primary production (VGP, open squares, mg O_2 m^{-3} d^{-1}) and volumetric respiration (VR, closed circles, mg O_2 m^{-3} d^{-1}) in the epilimnion of (A) Lac Croche and (B) Lac à l'Ours measured by bottle incubations. Solid black line shows VGP as calculated from the YTOTAL program (Fee et al. 1998). Grey line shows VGP:VR relative to the secondary y axis and the dotted line shows equal production and respiration rates. Error bars are at the α=0.05 critical level.

GPP from the $\delta^{18}O$ method–

The degree of saturation of oxygen in the epilimnion of Lac Croche between May 2002 and March 2003 varied from 60.0 to 109.8% and averaged 97.2% (Table 1-4). In Lac à l'Ours it ranged from 59.8 to 107.9%, with an average value of 94.3% (Table 1-5). In both lakes the degree of saturation oscillated around equilibrium until ice cover, when it gradually declined. The isotopic composition of oxygen in water, $\delta^{18}O_W$, in Lac Croche varied from –7.77 to –10.21‰ and averaged –8.33‰. In Lac à l'Ours values ranged from –7.77 to –10.21‰ and averaged –8.98‰. The isotopic composition of DO, $\delta^{18}O_{DO}$, in Lac Croche varied from 17.9‰ to 25.4‰ and averaged 20.9‰. Values in Lac à l'Ours ranged from 17.1 to 24.6 and averaged 20.6‰. In both lakes the most positive values occurred late in the winter and the lowest values occurred during the summer.

For all samples collected the degree of oxygen saturation, $\delta^{18}O_{DO}$, $\delta^{18}O_W$, and respiration rates were used to calculate GPP from the $\delta^{18}O$ method (Tables 1-4 and 1-5). As respiration was only measured on a bi-monthly basis, respiration rates were linearly interpolated between sampling dates. After the lake froze in mid-November, the atmospheric flux of oxygen was set to zero in equations 4 to calculate GPP from the isotopic measurements (Tables 1-4 and 1-5).

In Lac Croche, GPP from the $\delta^{18}O$ method ranged from 4 ± 20 to 341 ± 78 mg O_2 m^{-3} d^{-1}. GPP peaked in mid-summer and was lowest in the winter months (Figure 1-3A). Average GPP over the ice-free season was 177 ± 15 mg O_2 m^{-3} d^{-1} and 100 ± 10 mg O_2 m^{-3} d^{-1} over the year. In Lac à L'Ours GPP ranged from 12 ± 13 to 710 ± 153 mg O_2 m^{-3} d^{-1} and peaked in early summer (Figure 1-3B). GPP averaged 356 ± 22 mg O_2 m^{-3} d^{-1} over the ice-free season and 194 ± 14 mg O_2 m^{-3} d^{-1} over the year.

Table 1-4. Physical, chemical and isotopic properties in the epilimnion of Lac Croche between May 2002 and March 2003. Temperature (°C); depth of mixed layer (Z, m); degree of oxygen saturation ($[O_2]/[O_2]_{sat}$); isotopic signature of dissolved oxygen ($\delta^{18}O_{DO}$, ‰); isotopic signature of oxygen in water ($\delta^{18}O_W$, ‰), measured respiration (R, mg O_2 m^{-3} d^{-1}), and GPP calculated from the $\delta^{18}O$ method (GPP, mg O_2 m^{-3} d^{-1}). Confidence intervals are shown at the α=0.05 critical level.

Lake	Date	T	Z	$\%[O_2]_{sat}$	$\delta^{18}O_{DO}$	$\delta^{18}O_W$	R	GPP
Croche	22-May	10.0	3.25	103.4	22.7	-9.44	70±18	46±42
	27-May	13.7	3.25	102.9	20.3	-9.30		176±90
	3-Jun	14.3	3.25	102.0	18.6	-9.19	104±18	281±114
	10-Jun	16.9	3.25	103.3	18.1	-9.14		311±114
	20-Jun	16.6	3	101.9	19.0	-9.33	138±28	261±65
	26-Jun	19.7	2.25	103.4	20.9	-9.03		172±93
	1-Jul	24.2	2.5	103.9	19.8	-8.78	244±30	209±44
	8-Jul	23.0	2.75	105.7	17.9	-8.63		341±78
	15-Jul	22.4	3	104.1	18.9	-8.37	227±22	226±80
	23-Jul	22.9	3	109.8	18.9	-7.95		248±80
	29-Jul	21.3	3.5	101.3	18.1	-8.06	202±12	238±51
	7-Aug	21.4	4.25	104.6	20.7	-7.92		188±80
	11-Aug	22.3	4	103.8	18.5	-7.80	120±12	230±45
	23-Aug	21.6	4	104.9	18.6	-7.55	95±22	243±71
	29-Aug	20.9	4	104.6	20.9	-7.71		99±120
	3-Sep	21.0	4.25	103.5	21.3	-7.64	134±22	58±65
	11-Sep	21.8	4.75	105.3	20.0	-7.58		128±112
	17-Sep	18.4	4.75	103.9	20.7	-7.75	43±18	121±53
	25-Sep	18.0	5	104.9	22.3	-7.72		57±140
	1-Oct	15.9	6.75	101.1	22.1	-7.79	19±22	47±82
	9-Oct	13.2	6.75	104.7	21.0	-7.70		84±65
	16-Oct	11.2	7.75	104.7	22.0	-7.82		45±65
	23-Oct	8.3	8	100.0	23.1	-8.14	15±18	19±86
	30-Oct	6.1	8	104.3	19.4	-8.11		102±94
	6-Nov	3.9	8	99.5	20.7	-8.33	26±28	61±19
	13-Nov	4.0	8	105.3	22.0	-7.99		37±52
	4-Dec	2.8	8	102.9	20.0	-8.20	14±50	9±34
	11-Dec	2.6	8	95.2	23.7	-8.37		7±51
	9-Jan	3.5	8	86.2	22.5	-8.24		6±53
	15-Jan	2.6	8	77.3	22.9	-8.24		5±52
	21-Jan	3.3	8	87.4	23.5	-8.12	-7.1±33	4±20
	29-Jan	3.5	8	78.8	21.0	-8.25		8±57
	5-Feb	3.4	8	77.4	22.2	-8.22	19±52	11±33
	12-Feb	3.5	8	76.1	25.4	-8.23		10±56
	13-Mar	3.8	8	62.2	23.7	-8.26	62±44	10±27
	19-Mar	3.7	8	60.1	24.3	-8.17	-47±48	9±29

Table 1-5. Physical, chemical and isotopic properties in the epilimnion of Lac à l'Ours between May 2002 and March 2003. Temperature (°C); depth of mixed layer (Z, m); degree of oxygen saturation ($[O_2]/[O_2]_{sat}$); isotopic signature of dissolved oxygen ($\delta^{18}O_{DO}$, ‰); isotopic signature of oxygen in water ($\delta^{18}O_W$, ‰), measured respiration (R, mg O_2 m^{-3} d^{-1}), and GPP calculated from the $\delta^{18}O$ method (GPP, mg O_2 m^{-3} d^{-1}) . Confidence intervals are shown at the α=0.05 critical level.

Lake	Date	T	Z	$\%[O_2]_{sat}$	$\delta^{18}O_{DO}$	$\delta^{18}O_W$	R	GPP
à l'Ours	22-May	8.7	4.75	97.6	17.7	-10.20	77±0.2	316±13
	27-May	14.8	3.5	107.5	19.8	-10.21		277±56
	3-Jun	15.4	2.75	99.9	18.2	-10.20	294±30	434±63
	10-Jun	17.7	2.25	104.8	17.1	-9.89		709±153
	20-Jun	19.6	2.25	107.9	21.0	-9.87	337±44	587±83
	26-Jun	21.3	2.25	105.4	18.2	-9.59		570±175
	1-Jul	27.4	2.25	102.0	18.2	-9.25	404±16	573±116
	8-Jul	22.4	2.25	105.0	19.8	-9.08		406±143
	15-Jul	21.8	2.5	101.5	18.5	-8.94	358±20	471±53
	23-Jul	22.2	2.75	102.1	18.3	-8.63		471±94
	29-Jul	24.0	2.75	105.5	18.3	-8.32	241±26	529±63
	7-Aug	21.1	2.75	104.7	20.6	-8.35		312±110
	11-Aug	24.7	2.75	105.9	20.4	-7.92		338±108
	23-Aug	20.9	2.75	105.3	20.6	-7.89	263±28	307±64
	29-Aug	20.4	2.75	105.3	21.7	-7.94		221±133
	3-Sep	20.9	3	102.1	21.1	-7.77	256±40	232±76
	11-Sep	19.2	3.25	98.5	20.5	-7.81		242±192
	17-Sep	17.9	3.75	105.2	20.8	-8.19	238±54	181±116
	25-Sep	17.5	3.75	106.3	21.1	-8.09		193±197
	1-Oct	16.1	4	104.0	22.4	-8.15	147±40	120±77
	9-Oct	11.9	5.75	104.3	20.5	-8.42		141±142
	16-Oct	9.7	7.25	104.1	18.9	-8.70		163±142
	23-Oct	7.4	10.5	105.7	17.1	-9.03	58±30	147±78
	30-Oct	5.5	10.5	81.7	22.0	-9.13		51±86
	6-Nov	3.1	12	89.7	21.9	-9.14	16±28	57±22
	13-Nov	3.6	12	101.2	21.5	-9.27		30±123
	4-Dec	2.4	12	96.3	22.5	-9.33	22±156	12±95
	11-Dec	2.4	12	77.7	23.5	-9.25		13±101
	18-Dec	2.4	12	82.4	21.8	-9.06		14±107
	9-Jan	2.6	12	73.3	20.7	-9.30		15±110
	15-Jan	2.5	12	68.8	22.7	-9.46		14±103
	21-Jan	2.5	12	88.3	23.3	-9.77		14±100
	29-Jan	2.5	12	79.6	24.6	-9.44		15±97
	5-Feb	2.5	12	78.2	22.1	-9.63	-40±14	16±9
	12-Feb	2.5	12	76.9	22.7	-9.43		17±35
	26-Feb	2.5	12	59.8	21.8	-9.37	30±44	17±30
	13-Mar	2.4	12	62.8	20.9	-9.44		18±42
	19-Mar	2.5	12	60.6	24.1	-9.44	-1.6±22	16±13

From the $\delta^{18}O$ method, production dominated over respiration in Lac Croche throughout the summer and the ratio of GPP to R was highest in the fall during turnover. In Lac à l'Ours, GPP:R was highest in the spring and fall and near equilibrium in mid-summer. In the winter months, GPP:R was below 1 in both lakes. Average GPP:R was calculated from the ratio of total photosynthesis, ΣGPP and total respiration ΣR over the season. Both ΣGPP and ΣR were estimated by linear interpolation between sampling dates. Average GPP:R over the ice-free period was 1.5 ± 0.5 in Lac Croche and 1.4 ± 0.1 in Lac à l'Ours.

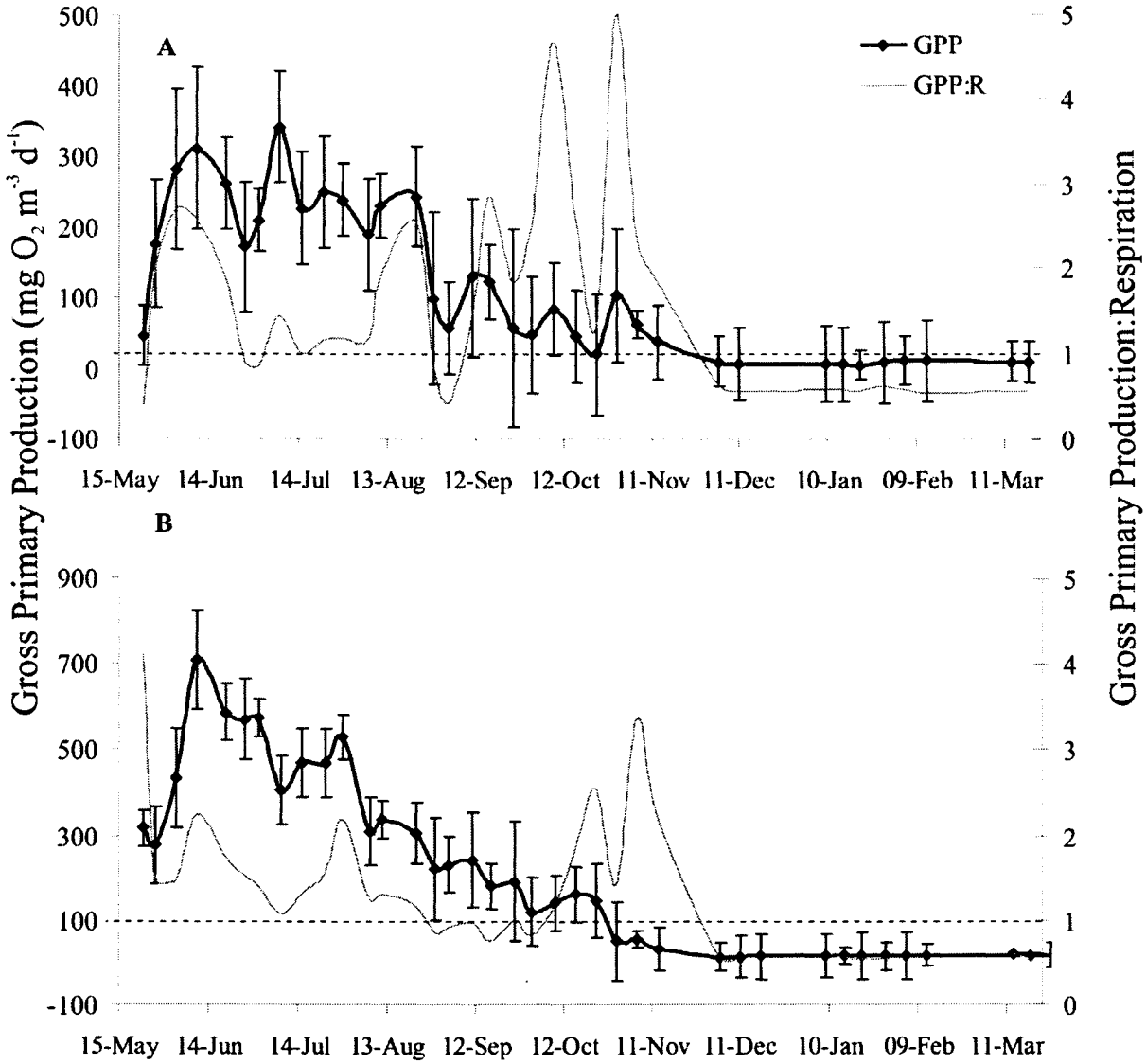

Figure 1-3. Gross primary production (black line) from the $\delta^{18}O$ method in (A) Lac Croche and (B) Lac à l'Ours between May 2002 and March 2003. Grey line shows GPP:R relative to the secondary y axis and the dotted line indicates equal amounts of production and respiration. Error bars are at the α=0.05 level.

GPP and R from the $\delta^{13}C$ method–

Over the ice-free season, both lakes were continually oversaturated in carbon dioxide, averaging 219% in Lac Croche and 294% in Lac à l'Ours (Table 1-6). $\delta^{13}C_{DIC}$, was slightly

lighter than the isotopic composition of dissolved atmospheric CO_2 in Lac Croche (averaging –12.7‰) and within the range of atmospheric values in Lac à l'Ours (averaging –7.87‰).

In Lac Croche, GPP calculated from the $\delta^{13}C$ method ranged from 16 to 334 mg O_2 m^{-3} d^{-1} and averaged 196 ± 23 mg O_2 m^{-3} d^{-1}, while respiration ranged from 2 to 261 and averaged 95 ± 24 mg O_2 m^{-3} d^{-1} (Figure 1-4A). GPP was highest in mid-summer and lowest in late fall. In Lac à l'Ours, GPP ranged from 76 to 386 mg O_2 m^{-3} d^{-1} and averaged 255 ± 30 mg O_2 m^{-3} d^{-1} (Figure 1-4B). GPP was low in the spring, highest in mid summer, and gradually declined over the fall months. Respiration in Lac à l'Ours ranged from 4 to 277 mg O_2 m^{-3} d^{-1} and averaged 118 ± 30 mg O_2 m^{-3} d^{-1}.

Calculations from the $\delta^{13}C$ method showed GPP was greater than R in both lakes Croche and à l'Ours over the entire ice-free season. In Lac Croche average GPP:R as calculated from $\Sigma GPP/\Sigma R$ was 2.0 ± 0.2. Average GPP:R in Lac à l'Ours was 2.2 ± 0.3.

Table 1-6. Carbon variables used to calculate GPP and R from the $\delta^{13}C$ method. Temperature (T, °C), pH, isotopic fractionation due to dissolution of CO_2 ($\varepsilon_{aq\text{-}g}$, ‰), carbon dioxide saturation ($[CO_2]_{sat}$, %), isotopic composition of dissolved inorganic carbon, carbon dioxide, and organic carbon ($\delta^{13}C_{DIC}$, $\delta^{13}C_{CO2}$, $\delta^{13}C_{DOC}$, ‰), respiration and gross primary production (R, GPP, mg O_2 m^{-3} d^{-1}).

Lake	Date	T	pH	$\varepsilon_{g\text{-}aq}$	$[CO_2]_{sat}$	$\delta^{13}O_{DIC}$	$\delta^{13}C_{CO2}$	$\delta^{13}C_{DOC}$	R	GPP
Croche	22-May	10.0	6.00	-1.36	298	-10.70	-14.15	-26.98	109±65	97±65
	27-May	13.7	6.10	-1.38	209	-19.74	-22.53	-26.62	78±23	194±23
	10-Jun	14.3	6.10	-1.39	220	-17.78	-19.12	-26.32	157±24	263±24
	20-Jun	16.9	6.12	-1.39	219	-18.29	-21.32	-26.33	277±26	267±26
	26-Jun	16.6	6.12	-1.41	189	-17.57	-17.71	-26.96	212±27	265±28
	1-Jul	19.7	6.19	-1.43	195	-18.78	-19.43	-26.22	224±36	262±36
	8-Jul	24.2	6.21	-1.42	154	-19.36	-19.43	-27.84	251±37	280±37
	15-Jul	23.0	6.25	-1.42	131	-9.39	-11.73	-26.19	133±34	334±34
	23-Jul	22.4	6.29	-1.42	163	-9.08	-10.18	-23.30	177±31	292±31
	29-Jul	22.9	6.24	-1.41	195	-10.42	-13.81	-25.99	195±32	284±32
	7-Aug	21.3	6.19	-1.41	195	-9.56	-11.75	-26.09	189±27	280±27
	11-Aug	21.4	6.19	-1.42	183	-14.23	-16.88	-26.29	72±23	222±23
	23-Aug	22.3	6.21	-1.42	200	-13.80	-17.41	-26.39	88±26	229±26
	29-Aug	21.6	6.18	-1.41	187	-15.47	-17.52	-26.28	74±25	229±25
	3-Sep	20.9	6.19	-1.41	190	-16.33	-18.38	-27.43	27±24	150±24
	11-Sep	21.0	6.19	-1.42	174	-10.90	-12.95	-25.41	48±23	132±23
	17-Sep	21.8	6.21	-1.40	199	-9.33	-10.32	-24.05	67±21	147±21
	25-Sep	18.4	6.15	-1.40	190	-11.30	-11.84	-26.28	58±20	124±20
	1-Oct	18.0	6.15	-1.39	262	-10.86	-11.68	-26.91	48±19	62±19
	9-Oct	15.9	6.07	-1.37	326	-11.87	-13.76	-25.28	4±16	57±16
	16-Oct	13.2	5.99	-1.36	347	-8.60	-9.42	-26.43	45±28	79±28
	23-Oct	11.2	5.96	-1.35	312	-8.98	-10.06	-26.38	65±19	49±19
	30-Oct	8.3	5.96	-1.34	296	-9.57	-11.22	-26.99	66±19	16±19
Ours	22-May	8.7	6.06	-1.35	215	-9.4	-11.6	-27.0	77±61	188±61
	27-May	14.8	6.15	-1.38	172	-8.1	-10.5	-28.2	77±65	196±65
	3-Jun	15.4	6.19	-1.39	150	-7.1	-9.8	-28.2	133±38	327±38
	10-Jun	17.7	6.19	-1.41	250	-5.3	-7.6	-27.7	245±94	486±94
	20-Jun	19.6	6.05	-1.41	335	-5.7	-7.7	-29.4	219±60	423±60
	26-Jun	21.3	6.14	-1.44	264	-8.1	-10.7	-27.1	245±44	416±44
	1-Jul	27.4	6.15	-1.42	279	-9.0	-11.2	-26.9	281±39	413±39
	8-Jul	22.4	6.19	-1.42	203	-9.9	-12.5	-27.9	148±68	316±68
	15-Jul	21.8	6.18	-1.42	209	-7.4	-10.0	-28.5	181±70	362±70
	23-Jul	22.2	6.20	-1.43	194	-7.1	-9.8	-24.4	184±35	331±35
	29-Jul	24.0	6.14	-1.41	265	-9.3	-11.6	-29.4	193±78	349±78
	7-Aug	21.1	6.14	-1.43	246	-7.8	-10.4	-28.3	76±79	221±79
	11-Aug	24.7	6.21	-1.41	191	-6.6	-9.2	-28.9	82±91	238±91
	23-Aug	20.9	6.14	-1.41	236	-8.2	-10.6	-30.0	70±84	224±84
	29-Aug	20.4	6.16	-1.41	215	-7.8	-10.3	-28.3	31±99	166±99
	3-Sep	20.9	6.16	-1.40	217	-7.5	-9.9	-29.5	39±50	178±50
	11-Sep	19.2	6.13	-1.40	232	-8.0	-10.2	-26.1	67±56	185±56
	17-Sep	17.9	6.01	-1.37	372	-5.3	-7.1	-26.4	57±84	149±84
	25-Sep	17.5	6.06	-1.36	293	-4.6	-6.6	-26.2	57±48	139±48
	1-Oct	16.1	6.00	-1.35	352	-6.4	-8.0	-26.7	12±29	76±29
	9-Oct	11.9	5.90	-1.34	464	-6.4	-7.5	-26.9	46±21	96±21
	16-Oct	9.7	5.89	-1.33	459	-8.0	-9.1	-26.5	66±40	105±40
	23-Oct	7.4	5.86	-1.34	478	-9.3	-10.1	-26.7	67±41	90±41

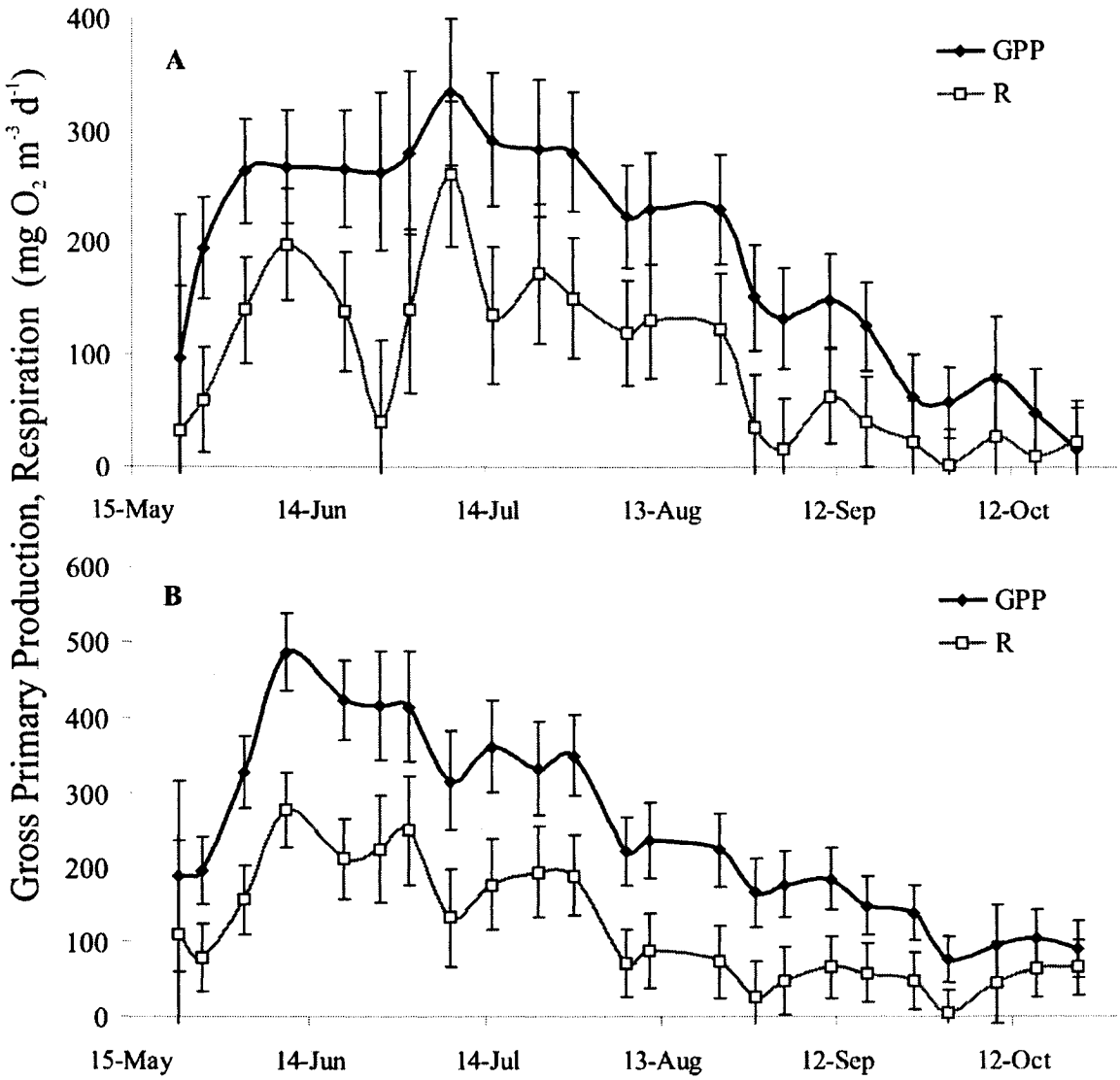

Figure 1-4. Gross primary production (closed circles, mg O_2 m^{-3} d^{-1}) and respiration (open squares mg O_2 m^{-3} d^{-1}) from the $\delta^{13}C$ method in lakes Croche (A) and à l'Ours (B) over the ice-free season of 2002. Error bars are at the α=0.05 critical level.

By assuming that the isotopic signature of respired carbon is equal to that of DOC, the $\delta^{13}C$ method implies that all organic carbon in the system is respired equally. $\delta^{13}C_{DOC}$ in lakes Croche and Ours averaged –26.2±0.2 and –26.6±0.1‰, in the mid-range of terrestrial C3 vegetation. If instead we assume that all carbon respired has the isotopic composition of autochthonous organic carbon, that is the isotopic signature of dissolved CO_2 plus

fractionation during photosynthesis, 20‰ (Laws et al. 1995), estimates of R in Lac Croche and Lac à l'Ours decrease by 23% and 5% respectively. Estimates of GPP increase by 7 and 1% in lakes Croche and à l'Ours.

Comparing methods –

In Lac Croche, mean GPP over the ice-free period was 188 ± 16 mg O_2 m^{-3} d^{-1} as measured by bottle incubations, 177 ± 15 mg O_2 m^{-3} d^{-1} as calculated from the $\delta^{18}O$ method, and 196 ± 23 as calculated from the $\delta^{13}C$ method (Figure 1-5A). A t-test for means with unequal standard errors was used to compare means measured by the different methods. There was no statistically significant difference in mean GPP in Lac Croche as measured by bottle incubations and the $\delta^{18}O$ method (t=0.13, df=30, p=0.89) or between bottle incubations and the $\delta^{13}C$ method (t=0.28, df=28, p=0.78). In Lac à l'Ours mean GPP was 357 ± 41 mg O_2 m^{-3} d^{-1} as measured by bottle incubations, 356 ± 22 mg O_2 m^{-3} d^{-1} as calculated from the $\delta^{18}O$ method, and 255 ± 30 mg O_2 m^{-3} d^{-1} as calculated from the $\delta^{13}C$ method (Figure 1-5B). There was no significant difference in the mean GPP from bottle incubations and the $\delta^{18}O$ method (t=0.10, df=28, p=0.92) or in mean GPP between bottle incubations and the $\delta^{13}C$ method (t=1.11, df=29, p=0.28).

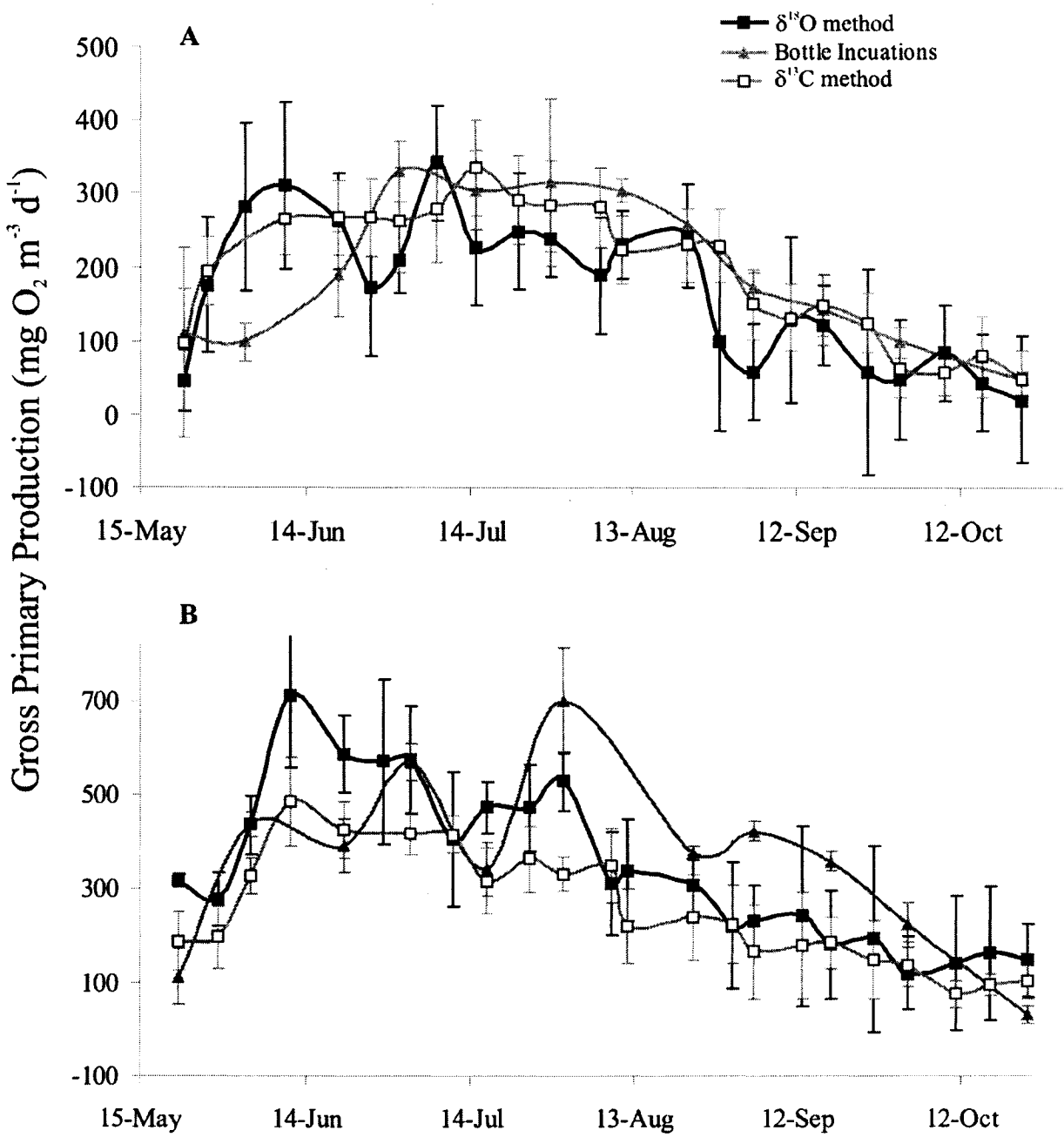

Figure 1-5. GPP (mg O_2 m^{-3} d^{-1}) measured from bottle incubations (closed triangles), the $\delta^{18}O$ method (closed squares) and the $\delta^{13}C$ method (open squares) in Lac Croche (A) and Lac à l'Ours (B). Error bars are at the α=0.05 significance level.

Respiration in Lac Croche as measured from bottle incubations averaged 122 ± 19 mg O_2 m^{-3} d^{-1} and 96 ± 23 mg O_2 m^{-3} d^{-1} from the $\delta^{13}C$ method (Figure 1-6A). In Lac à l'Ours, R averaged 252 ± 22 mg O_2 m^{-3} d^{-1} from bottle incubations and 118 ± 30 mg O_2 m^{-3} d^{-1} from the $\delta^{13}C$ method (Figure 1-6B). A t-test for means with unequal standard errors shows that the difference in mean R in either lake is not significant at the α=0.05 critical level (t=0.40, df=31, p=0.69 for Lac Croche and (t=1.70, df=29, p=0.10 in Lac à l'Ours).

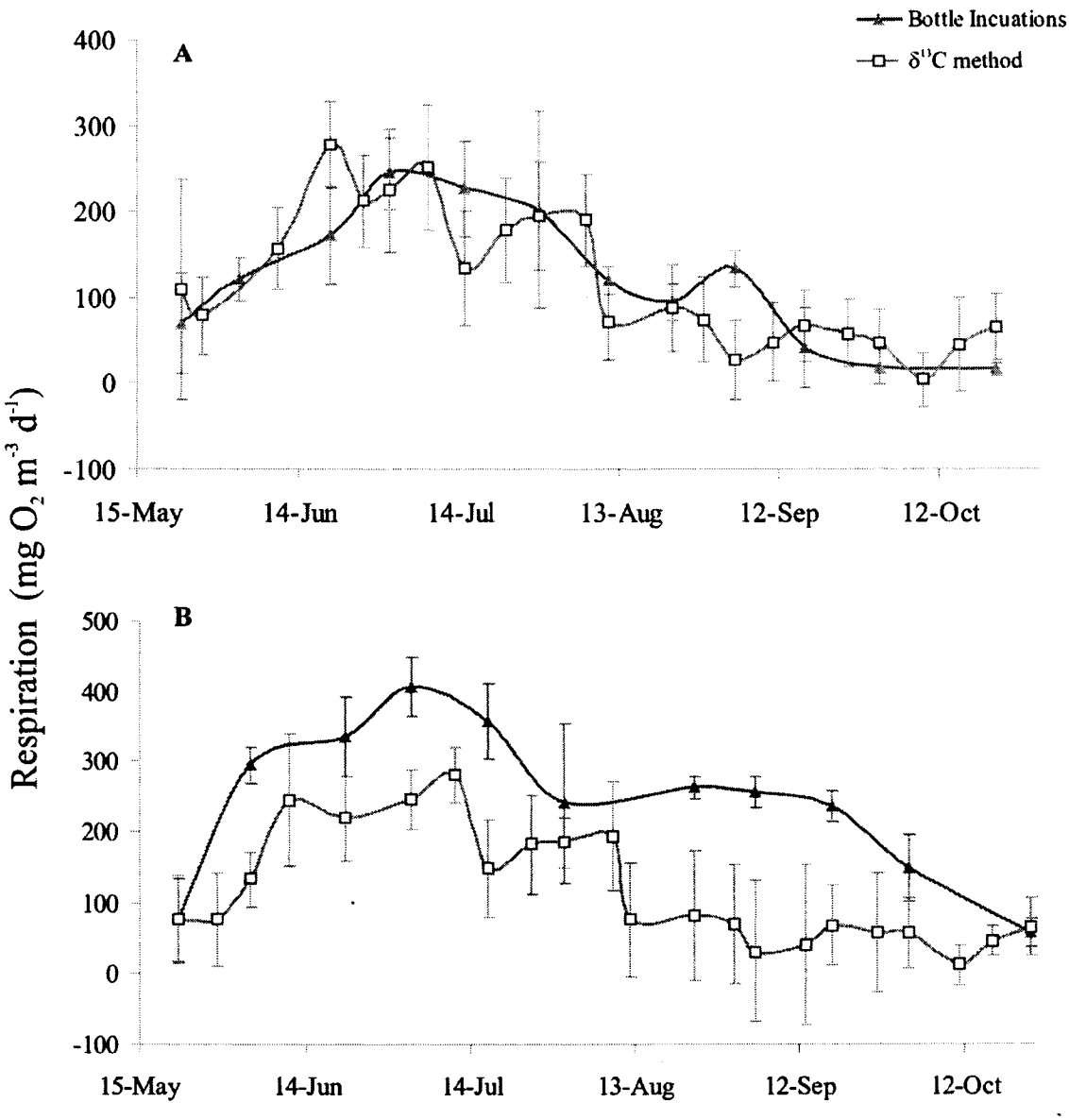

Figure 1-1-6. R (mg O_2 m^{-3} d^{-1}) measured from bottle incubations (closed triangles) and the $\delta^{13}C$ method (open squares) in Lac Croche (A) and Lac à l'Ours (B) over the ice free season of 2002. Error bars are at the α=0.05 significance level.

Though there is no statistical difference between average GPP from bottle incubations and from the $\delta^{18}O$ method, the two methods are not completely interchangeable and some differences between the two methods can be seen during the ice-free season

(Figure 1-6). Bottle incubations are point estimates of GPP while the isotopic signature of dissolved oxygen integrates samples over a longer period of time. However, because the $\delta^{18}O$ method still uses bottle estimates of R, benthic respiration is not taken into account and the oxygen isotope estimate of GPP is not of the entire aquatic system.

There is also no significant difference in mean GPP and R as measured from bottle incubations or the $\delta^{13}C$ method, but differences can be seen over the sampling period (Figure 1-5 and 1-6). To a degree, this should be expected as $\delta^{18}O_{DO}$ and $\delta^{13}C_{DIC}$ are influenced by photosynthesis of littoral macrophytes (negligible in Lac Croche) and by respiration in sediments. These components are integrated into the isotopic compositions of DO and DIC by epilimnetic mixing and thus included in the estimate of GPP from oxygen and carbon isotopes. Hence, our estimate of GPP from oxygen and carbon isotopes is an estimate of GPP for the whole mixed layer. Estimations of GPP made from bottle incubations do not include these components to any extent and they are only partially included in estimates from the oxygen isotope method.

However, estimates of R from the $\delta^{13}C$ method are frequently lower than estimates from bottle incubations. Both lakes were consistently oversaturated in carbon dioxide even when oversaturated in oxygen, suggesting that the model for DIC (equation 8) does not sufficiently describe carbon dynamics in the lakes. It is possible that allochthonous inputs of DIC, which are not taken into account in our model are masking the carbon isotopic signal from respiration. To test this hypothesis, a sensitivity analysis of the model was preformed with a hypothetical external input of DIC added to the equation 8. We measured $\delta^{13}C_{DIC}$ of groundwater in six wells surrounding Lac Croche and obtained an average value of −19.24 ‰. Assuming allochthonous inputs of DIC to be 5% of the total DIC, the model showed

average increases in R of 17% in Lac Croche and 35% in Lac à l'Ours. The same procedure decreased the estimates of GPP by 9% in lakes Croche and à l'Ours. The magnitude of R estimates from the $\delta^{13}C$ method are therefore very sensitive to external inputs of DIC while estimates of GPP from the $\delta^{13}C$ method are less sensitive to external inputs.

All three methods showed that production was greater than respiration over the ice-free season in Lac Croche. Average GPP:R was calculated as total GPP during the ice free season divided by total respiration over the ice-free season. GPP:R averaged 1.8 ± 0.6 as measured by the bottle incubations, 1.5 ± 0.4 as calculated from the $\delta^{18}O$ method and 1.0 ± 0.2 as calculated from the $\delta^{13}C$ method. A t-test for means with unequal standard errors showed no statistically significant difference between the mean GPP:R from bottle incubations and the $\delta^{18}O$ method (t=0.09, df=21, p=0.93) or from bottle incubations and the $\delta^{13}C$ method (t=0.32, df=31, p=0.75). All three methods also show a marked increase in the ratio of GPP to R in late fall when rates of respiration decreased more rapidly than rates of production. In Lac à l'Ours GPP:R averaged 1.3 ± 0.3 as measured by the bottles incubations, 1.4 ± 0.2 as calculated from the $\delta^{18}O$ method and 2.1 ± 0.3 as calculated from the $\delta^{13}C$ method. Again, a t-test showed no significant difference between GPP:R as measured by bottle incubations and the $\delta^{18}O$ method (t=0.11, df=23, p=0.92) or from bottle incubations and the $\delta^{13}C$ method (t=1.36, df=23, p=0.18).

Discussion

Traditional bottle incubation methods of estimating GPP and R in aquatic systems are labour intensive, require large incubators and large volumes of water. To estimate the metabolic balance over a long period of time, one must interpolate GPP from point samples

and from measurements that are subject to influence from rapid fluctuations in algal populations. Furthermore, this approach does not include metabolic contributions from littoral macrophytes and processes occurring near the sediment water interface.

Using stable isotopes to measure GPP eliminates the need for large incubators and large volumes of water. Advancements in automated analyses of $\delta^{18}O_{DO}$ (Barth et al. 2004) will improve the ease at which this method can be applied, as well as decrease its cost. In the $\delta^{18}O$ method, the variables $[O_2]$ and $\delta^{18}O_{DO}$ take into account littoral processes yet, because our measure of R is limited to planktonic R, the isotope measure of GPP also does not completely include contributions from macrophytes or benthic organisms. This study shows that the $\delta^{18}O$ method provides pelagic GPP estimates that are analogous to the traditional bottle incubation method. While the $\delta^{18}O$ method is appropriate for these oligotrophic lakes where the assumption that the aquatic system is sufficiently large to smooth short duration variations of $^{18}O_{DO}$, $^{18}O_W$, R, K_{O2}, O_2 and α_s is reasonable, a dynamic model may be required in systems with rapid fluctuations.

Estimates of GPP and R from the $\delta^{13}C$ method isotopes include benthic and littoral respiration, because these metabolic components influence the isotopic signatures and concentrations of dissolved oxygen and carbon dioxide. Furthermore, the isotope compositions integrate the effects of photosynthesis and respiration over the residence time of oxygen and carbon in the system. As a result, GPP and R estimates from stable isotopes are less sensitive to daily variations in GPP or R and the same number of samples will give a broader view of the metabolic balance of the system. The extent of this integration is dependent on the residence time of oxygen in the system; in summer months, when turnover is higher, the model integrates over a shorter period of time. Yet, the model is limited by the

assumed isotopic signature of respired carbon, $\delta^{13}C_R$, which may have a significant effect on estimates of GPP and R. However, the most severe limitation of the $\delta^{13}C$ method is that equation 8 does not adequately describe carbon dynamics in the lakes; external inputs of DIC are not accounted for. As shown, minor inputs of external carbon to the aquatic system will have a large effect on estimates of GPP and R from the $\delta^{13}C$ method. In systems with significant allochthonous carbon inputs, the $\delta^{13}C$ method cannot be accurate unless these inputs are accounted for.

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Chapter 2 Net Epilimnetic Autotrophy in Northern Temperate Lakes

Abstract

A stable isotope method that uses stable isotopes of oxygen, the degree of oxygen saturation and standard bottle incubation measurements of planktonic respiration (R) to measure gross primary production (GPP) in the epilimnion was used to determine metabolic balance of twenty-one lakes in three regions of Quebec and to examine underlying causes of the differences in lake metabolism. GPP dominated over R during the ice-free season, with respective GPP:R of 1.12±0.13. GPP:R varied significantly with time but there was more variation in GPP and R within lakes than between lakes. We did not find evidence that moderate levels of dissolved organic carbon (DOC), between 6 and 10 mg l^{-1} lead to net heterotrophy. Though our number of samples is limited, we did find net heterotrophy in lakes with DOC levels above 10 mg L^{-1}, where light penetration is severely limited by colored DOC.

Introduction

The balance between production and respiration lies at the basis of our understanding of carbon cycling and food web dynamics in aquatic systems. If production exceeds respiration, aquatic systems can act as sinks for carbon dioxide and as net sources of oxygen and organic matter. If aquatic systems are net heterotrophic, respiration exceeds production and they act as net sources of carbon dioxide to the atmosphere. However, the relative importance of primary production over community respiration in both marine and freshwater ecosystems has been a highly debated subject for many years. Some claim that allochthonous carbon fuels a large part of bacterial metabolism, that lakes are net sources of CO_2, and that the degree of net heterotrophy increases in unproductive aquatic ecosystems (del Giorgio et al. 1997; Duarte and Agustí 1998). This net heterotrophy hypothesis is

further supported by indirect evidence that lakes are commonly supersaturated in carbon dioxide and that bacteria can metabolize some allochthonous organic carbon input from a lake's watershed. Cole et al. (2000) found that respiration of allochthonous organic matter accounts for between 13 and 43% of total respiration. Other ecologists have considered aquatic systems to be fueled primarily by planktonic photosynthesis and have shown that even oligotrophic waters can be net autotrophic (Williams 1998; Carignan et al. 2000; Karl et al. 2003).

The debate is further confounded by widely varying results in a narrow geographic region. del Giorgio and Peters (1994) and Prairie et al. (2002) reported that respiration exceeds photosynthesis in the epilimnion of all but the most eutrophic lakes of the Eastern Townships region of Quebec. Carignan et al. (2000), on the other hand, found production to be greater than respiration in oligotrophic systems and concluded that allochthonous carbon metabolism is an insignificant source of CO_2 in twelve lakes in the Laurentian region of Québec. Meech Lake, north of Gatineau, Québec was found to be strongly production dominated in early-summer and strongly respiration dominated throughout the rest of the year (Wang and Veizer 2000, 2004). The reason for the difference in these findings is unclear, but may involve fundamental limnological differences.

Recent studies have examined the underlying relationships between the metabolic balance of lake epilimnia and allochthonous dissolved organic carbon. Prairie et al. (2002) attempted to resolve the difference between the Laurentian and Eastern Township lakes by explaining the metabolic balance in terms of a dissolved organic carbon gradient. Lakes with less than 4 to 6 mg L^{-1} DOC are net autotrophic while lakes above 6 mg L^{-1} DOC are net heterotrophic. However, Jannson et al. (2000) observed that Swedish lakes with concentrations of DOC up to 10 mg L^{-1} were net autotrophic. Using a model that considers

changes in gas concentrations as a function of GPP, R and diffusion, Hanson et al. (2003) measured GPP and R from changes in dissolved oxygen and carbon dioxide concentrations. They also found that DOC concentrations above 10 mg L^{-1} resulted in net heterotrophy.

Stable isotopes of dissolved oxygen can be used to examine the metabolic balance of aquatic systems (Quay et al. 1995; Luz et al. 2000; Chapter 1). Dissolved oxygen in equilibrium with atmospheric oxygen has a $\delta^{18}O$ signature of about 23.5‰ VSMOW. Respiration preferentially consumes the light isotope of oxygen and leaves the dissolved oxygen pool heavier while photosynthesis converts oxygen in a water molecule into O_2 without fractionation. Oxygen in H_2O in the study area has an isotopic composition of about −10‰, so production leaves the dissolved oxygen pool with a depleted isotopic composition. Traditional methods of measuring metabolic parameters in lakes give only estimates of planktonic respiration and production. In Chapter 1 two methods of using stable isotopes to measure metabolic parameters in lakes are proposed. The first uses stable isotopes of oxygen and the degree of oxygen saturation, and is directly comparable to traditional methods that measure planktonic respiration and production. The second stable isotope methodology uses isotopes of carbon and oxygen and is used to estimate metabolic balance, including littoral and benthic components. Here we sampled 21 lakes in three regions of Quebec between May and October of 2003 and use both methods to determine the metabolic balance of the lakes and to examine underlying causes of previously reported differences.

Methods

Study Site –

Twenty-one lakes in southern Quebec were sampled between May and October of 2003. Most of the lakes stratify and are ice covered between November and April. Catchments are forested primarily with sugar maple (*Acer saccharum*), yellow birch (*Betula*

alleghaniensis), beech (*Fagus grandifolia*) and poplar (*Populus tremuloïdes*). We sampled fourteen lakes in the Laurentians, located between 60 and 120 km northwest of Montreal on the Canadian Shield on a monthly basis between May and October. The area is underlain primarily by anorthositic bedrock covered by 1-5m of glacial till. We sampled two lakes in the Gatineau hills north of Ottawa, Ontario, in May, July and October of 2003. These lakes are also on the Canadian Shield and are underlain primarily by granites and marbles. Five lakes in the Eastern Townships region of Quebec were also sampled in May, July and October of 2003. The region is much different geologically and topographically from the other two regions. While some lakes sit on the sedimentary rocks of the St. Lawrence lowlands, metamorphic schists underlie others. Three of the lakes sampled in the Eastern Townships were strongly stratified while Lac Brome was only weakly stratified, and Lac Waterloo did not stratify. Physical parameters of these lakes are summarized in Table 2-1.

Table 2-1.Morphometric parameters of the twenty-one study lakes, lake area (LA, km^2), watershed area (WA, km^2), and mean depth (*zm*, m).

Lake	Region	Location	LA	WA	*zm*
Achigan	Laurentians	45°56'N, 74°00'W	5.31	96.50	12.7
de la Blanche	Laurentians	46°08'N, 74°44'W	0.41	3.95	10.5
Connelly	Laurentians	45°53'N, 73°58'W	1.24	24.36	7.8
En Coeur	Laurentians	45°58'N, 74°01'W	0.47	1.64	3.4
Gervais	Laurentians	46°16'N, 74°41'W	0.97	8.65	24.4
Montagne Noire	Laurentians	46°12'N, 74°16'W	2.80	13.16	13.0
du Nord	Laurentians	46°03'N, 74°02'W	0.87	13.95	7.9
Ouimet	Laurentians	46°10'N, 74°35'W	1.60	19.34	9.3
Pin Rouge	Laurentians	45°57'N, 74°02'W	0.15	7.06	4.9
de la Rouge	Laurentians	46°07'N, 74°42'W	0.68	12.12	8.1
des Sables	Laurentians	46°01'N, 74°15'W	2.96	40.61	9.3
St. Joseph	Laurentians	45°96'N, 74°33'W	1.47	60.22	12.1
Tremblant	Laurentians	46°12'N, 74°35'W	9.56	229.00	36.5
à la Truite	Laurentians	46°01'N, 74°15'W	0.51	4.24	8.9
d'Argent	Eastern Townships	45°29'N, 72°28'W	1.00	13.20	4.6
Bowker	Eastern Townships	45°42'N, 72°21'W	2.30	8.10	25.9
Brome	Eastern Townships	45°23'N, 72°49'W	14.50	185.70	5.8
Orford	Eastern Townships	45°29'N, 72°27'W	1.30	10.60	17.7
Waterloo	Eastern Townships	45°27'N, 74°68'W	1.50	31.60	2.9
la Pêche	Gatineau	45°59'N, 75°98'W	7.05	93.80	8.4
Phillippe	Gatineau	45°63'N, 76°18'W	1.72	18.40	6.6

Sampling –

Stable isotopes of dissolved oxygen, water, dissolved inorganic carbon, and dissolved organic carbon ($\delta^{18}O_{DO}$, $\delta^{18}O_W$, $\delta^{13}C_{DIC}$, $\delta^{13}C_{DOC}$), water chemistry and community respiration (R) were measured on a monthly basis in the fourteen Laurentian lakes between May and October of 2003. $\delta^{18}O_{DO}$, $\delta^{18}O_W$, $\delta^{13}C_{DIC}$, $\delta^{13}C_{DOC}$ and R were measured in May, July and October in the Gatineau and Eastern Township lakes. Water was collected with a 4 L Van Dorn bottle over the entire epilimnion (defined as the surface mixed layer where the vertical temperature gradient does not exceed 1 °C m^{-1}) and pooled in clean 20-L dark polyethylene containers. In Lake Waterloo, which did not stratify, the entire water column was sampled. Sub-samples were taken for stable isotope, chlorophyll *a* and DOC analysis. Samples for TP and TN were taken at 1, 3, and 5 meter intervals and averaged over the epilimnion on a monthly basis from the fourteen Laurentian lakes. Oxygen and temperature profiles were measured at half-meter intervals with a YSI Model 55 instrument, equipped with a stirrer. The probe was calibrated prior to each use in vapour-saturated air with respect to atmospheric pressure, within 2°C of epilimnetic temperature. The degree of oxygen saturation was calculated with respect to temperature and local barometric pressure according to Benson and Krause (1984). pH and alkalinity were measured in the field using a Hach field chemistry kit (Loveland, CO). The light extinction coefficient of the water column was measured (Li-Cor LI-192 and LI-190 sensors) at half-meter intervals. The amount of photosynthetically available radiation (PAR) was measured (Li-Cor LI-190) at Lac Croche and the values used to estimate PAR at the nearby lakes. In October, all lakes sampled were unstratified and October results reported here apply to the entire water column.

Chemical Analyses –

Chlorophyll was measured by spectrophotometery after overnight extraction of frozen GF/C filters in cold ethanol (Sartorg and Grobbelaar 1984) and corrected for phaeopigments. DOC was measured with an OI Analytical "TIC-TOC" Analyser Model 1010 according to St. Jean (2003). Persulfate is added to the sample to oxidize the organic carbon to CO_2 at 100°C, which is purged from the sample and measured at a nondispersive infrared detector. Replicate analyses had a standard deviation of 0.2 mg L^{-1}. Fifty mL samples for total phosphorus were autoclaved with 0.5 g potassium persulfate for 1 h at 120°C and measured with the molybdenum-blue method (Stainton et al. 1977). Total nitrogen was measured after alkaline persulfate digestion and cadmium reduction of 50 ml samples at 120°C.

Stable isotopes –

Samples for the isotopic composition of dissolved oxygen and water, $\delta^{18}O_{DO}$ and $\delta^{18}O_W$, of the epilimnion were collected in triplicate 10 mL Exetainers (VWR) with rubber septa, treated with $HgCl_2$ to prevent bacterial growth, stored at 4°C in the dark and analyzed within two months. Analysis was performed at the G. G. Hatch Isotope Laboratory at the University of Ottawa. For $\delta^{18}O_W$, one mL of sample was equilibrated with CO_2 at 25°C overnight and the resultant CO_2 was then analyzed on a triple collector VG SIRA 12 mass spectrometer, with a standard error of ±0.1‰. For $\delta^{18}O_{DO}$, samples were analyzed by creating a 5 ml helium headspace, equilibrating the water sample with the headspace and analyzing an aliquot of the resulting gas by isotope ratio mass spectrometry using a Delta XP and Gas Bench II from Thermo Finnigan (Barth et al. 2004) with a standard error of 0.4‰. Values are reported as ‰ VSMOW. Samples for $\delta^{13}C_{DIC}$ and $\delta^{13}C_{DOC}$ were analysed at the G. G. Hatch Isotope Laboratory on an OI Analytical "TIC-TOC" Analyser following the

procedure outlined by St. Jean (2003). Briefly, samples were first analysed for the concentration of organic and inorganic carbon and then for isotopic composition of DIC and DOC by helium carrying the resulting CO_2 organic/inorganic from the TIC-TOC analyser into a Finnigan Mat DeltaPlus isotope ration mass spectrometer for analysis by continuous flow. Standard deviation of isotope samples was 0.2‰. The isotopic composition of dissolved carbon dioxide, $\delta^{13}C_{CO2}$, was calculated from $\delta^{13}C_{DIC}$, pH and temperature using the fractionation equations of Zhang et al. (1995) and equations for temperature and pH dependent carbonate speciation (Drever, 1997).

- *Planktonic Respiration measurements (R)* –

Water was collected with a 4 L Van Dorn bottle over the entire epilimnion and pooled in clean 20 L dark polyethylene containers, mixed, distributed into quadruplicate clear 300 mL pyrex bottles that were used for measurement of the initial concentration of DO. A complementary set of quadruplicate dark 300 mL pyrex bottles were placed in an incubator at in situ temperatures for 6 to 8 hours. A high precision Winkler method was used to determine R from changes in dissolved oxygen in clear and dark bottles during the incubation (Carignan et al. 1998). The detection limits for R were 0.5 mg C m^{-3} h^{-1}. Daily volumetric (VR) and areal (AR) respiration rates were calculated assuming that respiration rates measured from water sampled in the morning were representative of the entire day.

Planktonic Production calculations –

Planktonic gross primary production (GPP) was calculated from $\delta^{18}O_{DO}$, $\delta^{18}O_W$ and R following the $\delta^{18}O$ method in Chapter 1. Briefly, both the concentration and isotopic composition of dissolved oxygen are a function of respiration, atmospheric exchange and production. By measuring the amount of respiration and atmospheric exchange, as well as

the isotopic composition of these components, an isotope mass balance equation can be used to calculate the amount of production. Variables required for the model described in Chapter 1 include the isotopic composition of dissolved oxygen and water ($\delta^{18}O_{DO}$, $\delta^{18}O_W$), respiration (R), temperature (T), concentration of dissolved oxygen ($[O_2]$), and depth of the mixed layer (e_z). In October, when all the lakes sampled were unstratified, the model was applied over the mean depth of the lake.

$\delta^{13}C$ metabolic balance method –

The $\delta^{13}C$ method described in Chapter 1 estimates GPP and R from carbon and oxygen concentrations and isotopic compositions. Because it does not rely on bottle estimates of R it includes the pelagic and littoral components of lake metabolism. However, as discussed in Chapter 1, the $\delta^{13}C$ method does not completely describe carbon dynamics in lakes and is inappropriate when allochtonous inputs of inorganic carbon into the lake are significant. To determine if the $\delta^{13}C$ method was appropriate for the lakes sampled in this study we examined the correlation between carbon dioxide and oxygen saturation and between $\delta^{18}O_{DO}$ and $\delta^{13}C_{CO2}$. A negative correlation between the pairs of variables suggests that production and respiration are the primary controls on inorganic carbon in the lakes. Of all the lakes sampled, $\delta^{13}C_{CO2}$ was never significantly negatively correlated with $\delta^{18}O_{DO}$ and carbon dioxide saturation was only significantly negatively correlated with oxygen saturation in Lac à la Truite. Resultantly we opted not to apply the $\delta^{13}C$ method to the lakes sampled in 2003.

Statistical Analyses –

Variables used in multiple linear regressions were tested against the standard normal distribution with a Chi-squared goodness of fit test Non-normal variables were log

transformed and used as such in multiple regressions. For multiple linear regressions, all regression parameters were bootstrapped 1000 times and standard errors are reported. Analysis of variance was used to determine if differences in variables were significant between the lakes sampled and between the months sampled. Because the Laurentian lakes were sampled more frequently than the other lakes, our analysis of variance models were imbalanced. Considering this, all ANOVAs were run twice, once with all the lakes included and only samples from May, July and October, when all the lakes were sampled, and once with only Laurentian lakes and all the months included and results for both are reported. Errors of measurements are reported as standard errors of replicates.

Results

Planktonic Gross Primary Production –

$\delta^{18}O_{DO}$ ranged from 19.1‰ to 24.7‰ and averaged 22.9‰ (Table 2), lighter than atmospheric equilibrium indicative of production dominance. On average $\delta^{18}O_{DO}$ was closest to atmospheric equilibrium in October and lightest in July and August. $\delta^{18}O_W$ ranged from –12.1‰ to –7.1‰ and averaged –9.8‰. Oxygen saturation in the lakes ranged from 79 to 120%, averaging 104%. All lakes were undersaturated in October while all were at saturation or oversaturated between June and September (Figure 2-1). When $\delta^{18}O_{DO}$ is plotted against % oxygen saturation (Figure 2-1), most cases fall on a mixing line. There are, however, instances when lakes are oversaturated in oxygen and have values of $\delta^{18}O_{DO}$ above or near atmospheric values of oxygen. This circumstance can arise when water temperature rises quickly and the flux of oxygen to the atmosphere lags behind. Oxygen oversaturation that is not the result of an excess of GPP over R will occur. The reverse situation will occur if water temperature decreases quickly.

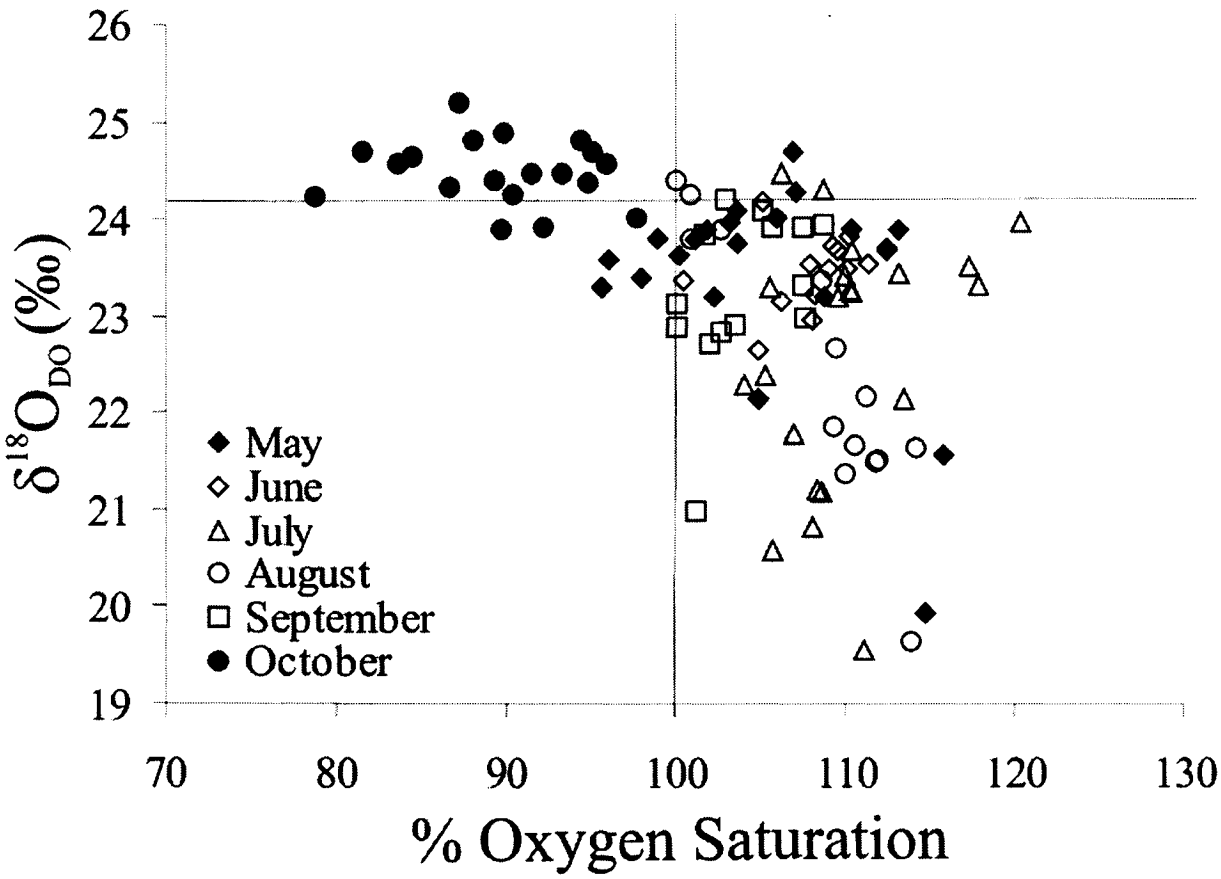

Figure 2-1. Isotopic composition of dissolved oxygen ($\delta^{18}O_{DO}$) and percent oxygen saturation of the lakes sampled between May and October 2003.

Table 2-2. Physical, chemical and metabolic properties of the mixed layer during the stratified period and of the water column under unstratified conditions. Temperature (T, °C), depth of mixed layer (Z, m), oxygen concentration ($[O_2]$, mg L^{-1}), degree of oxygen saturation (O_{2sat}), chlorophyll *a* (Chl-a, mg m^{-3}), dissolved organic carbon (DOC, g m^{-3}), conductivity (Cond, µS cm^{-1}), total phosphorus (TP, mg m^{-3}), total nitrogen (TN, mg m^{-3}), isotopic composition of dissolved oxygen and water ($\delta^{18}O_{DO}$, $\delta^{18}O_W$, ‰ VSMOW), volumetric respiration and production (R, GPP, mg O_2 m^3 d^{-1}), and metabolic balance (GPP:R).

Lake	Date	T	Z	$[O_2]$	O_{2sat}	Chla	DOC	Cond	TP	TN	$\delta^{18}O_{DO}$	$\delta^{18}O_W$	R	GPP	GPP:R
Achigan	22-May	13.68	4	10.74	1.07	2.09	5.3	53	6.3	307	24.2	-10.6	196±31	134±29	0.7±0.3
	16-Jun	17.50	4	10.15	1.10	2.56	3.7	55	4.5	314	23.3	-10.5	211±38	190±37	0.9±0.4
	30-Jun	23.50	3.5	9.60	1.18	2.22	3.8	57	5.1	300	22.8	-9.0	277±61	294±64	1.1±0.5
	30-Jul	21.00	5.5	9.57*	1.00	2.60	3.5	58	3.5	230	23.9	-9.7	121±48	104±54	0.9±1.3
	11-Sep	19.00	5.5	9.65	1.08	2.01	3.6	59	4.9	202	22.8	-9.4	67±21	100±18	1.5±0.7
	29-Oct	7.00	n.s.	11.01	0.95	1.50	3.9	56	5.2	295	23.9	-9.7	93±37	64±28	0.7±0.4
Blanche	15-May	9.33	4.5	11.26	1.01	0.46	4.6	28	4.1	280	23.3	-10.4	6.9±12	42±12	6.1±1.3
	11-Jun	16.20	3	9.91	1.05	1.45	2.4	28	3.4	254	23.7	-10.3	244±20	198±24	0.8±0.2
	1-Jul	22.00	3	8.81	1.06	1.71	2.6	28	2.9	225	22.8	-8.8	248±32	271±36	1.1±0.2
	2-Aug	21.20	5	9.33	1.09	1.30	2.5	29	3.9	254	22.2	-9.6	125±27	173±28	1.4±0.5
	9-Sep	18.00	6	9.41	1.03	1.97	2.7	28	5.4	147	23.7	-9.2	101±15	85±14	0.8±0.2
	27-Oct	7.70	n.s.	10.48	0.92	1.20	2.7	28	4.1	260	23.4	-9.8	139±25	101±20	0.7±0.2
Connely	20-May	16.23	3	10.66	1.13	3.06	5.8	126	8.3	370	23.2	-11.1	188±23	200±28	1.1±0.3
	16-Jun	16.30	3	10.03	1.06	2.59	4.4	133	7.5	343	22.7	-10.9	266±15	276±19	1.0±0.1
	30-Jun	24.70	3	9.58	1.20	2.79	4.4	138	7.6	290	23.5	-9.4	398±31	347±41	0.9±0.2
	30-Jul	22.00	3	9.04*	1.07	2.40	4.7	141	5.4	284	23.8	-10.0	190±25	180±40	1.0±0.6
	11-Sep	19.00	5	9.65	1.08	3.70	4.5	146	6.0	236	23.4	-9.5	247±23	202±15	0.8±0.1
En Coeur	23-May	11.90	3	10.48	1.02	1.80	6.2	20			23.4	-8.8	11±15	77±9	2.2±0.6
	9-Jun	17.74	4	10.25	1.13	2.56	5.6	62			23.2	-8.6	127±40	151±36	1.2±0.8
	4-Jul	23.50	3	8.72	1.08	3.02	3.1	15			20.7	-8.0	371±13	542±22	1.5±0.1
	2-Aug	22.20	3	9.00	1.09	4.22	4.9	32			22.9	-7.5	258±24	290±29	1.1±0.2
	8-Sep	19.00	5	9.16	1.02	3.41	4.0	32			22.2	-7.1	292±9	303±13	1.0±0.1
Gervais	15-May	9.83	3	11.40	1.04	5.29		46	6.5	210	23.3	-7.6	268±29	258±32	1.0±0.2

	10-Jun	17.02	4	10.05	1.09	2.11	2.5	46	4.0	195	23.3	-7.2	252±36	242±44	1.0±0.3
	2-Jul	23.00	4	8.99	1.10	0.66	2.5	46	3.3	167	22.8	-7.6	362±13	346±21	1.0±0.1
	29-Jul	20.70	5.5	8.70*	1.01	0.90	2.7	47	3.1	181	23.3	-7.9	143±33	135±38	1.0±0.7
	12-Sep	19.50	7	9.65	1.09	0.51	2.6	47	2.7	142	23.5	-7.7	55±28	67±27	1.2±1.3
	28-Oct	9.10	16	10.68	0.98	1.20	2.6	45	3.3	185	23.5	-8.0	63±23	49±17	0.8±0.4
Montagne Noire	15-May	9.08	4	12.68	1.13	2.29	2.9	35	4.7	260	23.4	-10.3	105±17	1204±21	1.1±0.5
	16-Jun	15.00	6	10.63	1.10	1.15	1.9	34	4.9	200	23.2	-10.1	365±68	279±75	0.8±0.3
	7-Jul	22.20	4	9.16	1.10	1.85	2.1	35	4.9	186	22.8	-7.4	154±10	199±16	1.3±0.2
	1-Aug	20.80	7	9.38	1.09	1.48	2.3	35	4.3	171	21.4	-9.6	134±6	181±9	1.3±0.1
	9-Sep	17.40	8.5	9.41	1.02	1.56	2.4	35	4.2	134	23.4	-9.4	144±31	117±28	0.8±0.3
	27-Oct	7.70	n.s.	10.15	0.89	1.40	2.2	34	4.7	210	23.9	-9.7	62±36	41±32	0.7±0.6
du Nord	20-May	15.94	2	10.53	1.11	2.61	7.0	52	7.7	319	23.4	-10.2	268±17	275±26	1.0±0.2
	18-Jun	19.00	3	9.27	1.05	2.05	5.5	54	10.9	318	22.2	-10.0	244±22	301±23	1.2±0.2
	4-Jul	23.20	3.5	8.57	1.06	2.20	5.5	56	8.6	319	20.1	-9.0	263±34	448±36	1.7±0.2
	1-Aug	22.50	4	9.19	1.11	3.38	5.3	58	8.7	311	21.2	-9.0	200±30	311±23	1.6±0.2
	11-Sep	18.00	5	9.41	1.03	4.09	5.3	58	6.2	241	22.4	-8.7	360±24	330±36	0.9±0.3
	19-Oct	6.20	n.s.	10.27	0.87	3.20	6.1	55	10.2	327	23.8	-9.0	42±16	30±29	0.7±0.7
Ouimet	12-May	10.30	2	10.45	0.96	6.46	7.8	74	9.5	321	23.1	-9.6	163±10	201±44	1.2±0.3
	10-Jun	17.98	3.5	9.72	1.08	2.05	4.3	79	9.2	275	23.0	-9.9	283±52	261±22	0.9±0.1
	4-Jul	22.50	3	8.91	1.09	2.01	4.1	81	6.6	255	20.7	-9.1	220±17	410±35	1.9±0.3
	29-Jul	21.50	4	9.70*	1.15	2.10	4.3	82	5.9	249	23.4	-9.1	151±12	159±30	1.1±0.6
	12-Sep	19.00	5	9.65	1.08	0.99	4.2	84	6.6	243	22.5	-8.9	192±12	209±17	1.1±0.2
	28-Oct	7.70	n.s.	10.15	0.90	6.40	4.5	79	7.3	318	23.4	-9.7	114±57	80±11	0.8±0.1
Pin Rouge	29-May	16.87	2	10.49	1.15	3.27	11.3	25			19.5	-11.4	373±45	749±60	2.0±0.3
	17-Jun	17.00	2	9.26	1.01	3.43	15.2	13			22.9	-10.8	397±32	377±20	0.9±0.1
	7-Jul	25.00	2	8.50	1.08	3.69	9.7	14			20.3	-9.8	284±69	618±22	2.2±0.1
	1-Aug	22.00	2	9.33	1.11	5.99	7.0	17			21.7	-9.6	296±22	482±27	1.6±0.1
	8-Sep	18.00	3	9.49	1.03	3.75	5.8	17			22.4	-8.9	330±16	352±52	1.1±0.3
	27-Oct	5.40	n.s.	9.49	0.79	4.03	7.5	17			23.8	-9.3	140±35	92±47	0.7±0.4
Rouge	15-May	9.31	3	11.49	1.03	2.59	3.9	27	5.8	285	23.5	-10.0	76±32	99±29	1.3±0.8
	11-Jun	16.20	4	10.28	1.09	1.41	2.3	27	4.3	257	23.0	-10.0	160±69	172±77	1.1±0.9
	1-Jul	22.20	3.5	9.14	1.10	2.24	2.5	27	4.6	216	22.9	-10.1	234±22	237±26	1.0±0.2
	5-Aug	23.00	6	9.33	1.14	1.61	2.5	28	4.0	184	21.2	-9.3	143±16	215±19	1.5±0.3
	9-Sep	19.00	7	9.41	1.05	1.32	2.7	29	4.5	204	23.6	-9.2	156±35	125±31	0.8±0.4
	27-Oct	7.90	n.s.	9.86	0.87	1.83	10.3	28			24.7	-9.5	90±18	43±23	0.5±0.3

des Sables	14-May	9.73	2	10.84	0.99	1.54		71	5.8	352	23.3	-11.9	110±28	143±28	1.3±0.3
	9-Jun	16.70	4.5	10.24	1.10	0.99	2.7	74	5.8	291	23.0	-11.0	154±17	158±21	1.0±0.2
	3-Jul	22.70	4	8.97	1.10	2.63	2.9	74	7.0	263	22.7	-11.2	272±44	255±39	0.9±0.3
	5-Aug	21.70	5	9.36	1.12	3.31	2.9	74	5.5	225	21.0	-10.0	175±17	260±19	1.5±0.2
	10-Sep	18.00	6.5	9.16	1.00	2.70	3.3	80	5.1	208	22.4	-9.7	196±21	187±18	1.0±0.1
	26-Oct	6.80	n.s.	10.48	0.90	2.23	5.3	74			23.8	-9.9	101±40	70±32	0.7±0.4
St. Joseph	22-May	13.75	5	10.39	1.04	1.98		55	8.5	449	23.6	-11.6	145±24	116±21	0.8±0.3
	16-Jun	18.50	4	9.74	1.08	2.78	3.3	63	6.5	404	22.5	-11.3	387±70	340±66	0.9±0.3
	3-Jul	23.20	3	9.01	1.11	2.09	3.4	67	8.8	345	19.1	-10.6	222±22	528±326	2.4±0.2
	5-Aug	22.40	4	9.24	1.12	3.21	3.3	71	5.4	282	21.0	-10.3	209±23	313±24	1.5±0.2
	10-Sep	18.00	6	9.16	1.00	3.42	3.8	71	7.0	330	22.6	-9.9	248±26	216±23	0.9±0.1
	26-Oct	6.70	n.s.	9.82	0.84	1.10	4.2	53	6.5	348	24.2	-9.6	10±28	16±22	0.5±0.8
Tremblant	12-May	4.83	n.s.	11.85	0.98	0.30		39	4.2	343	22.9	-11.2	25±22	22±17	0.9±0.5
	12-Jun	12.72	10	11.31	1.11	1.15	3.0	38	3.6	350	23.1	-11.2	36±27	51±20	1.4±1.1
	2-Jul	21.00	4	9.94	1.17	1.39	2.9	38	3.1	334	23.0	-11.9	115±21	143±25	1.2±0.3
	6-Aug	22.00	7	9.16	1.10	1.21	3.2	39	3.2	315	20.9	-10.7	50±32	132±29	2.6±1.9
	12-Sep	19.00	9	9.49	1.06	1.94	3.3	39	2.7	287	23.4	-10.5	71±41	65±34	0.9±0.9
	28-Oct	9.30	n.s.	10.15	0.93	0.60	3.5	36	3.1	314	24.0	-10.8	75±30	48±21	0.6±0.5
Truite	14-May	9.00	3	11.18	1.00	1.43	4.7	254	7.3	308	23.2	-10.4	143±23	156±24	1.1±0.2
	9-Jun	16.28	5	10.15	1.08	0.97	2.6	267	3.7	286	22.7	-9.9	118±20	141±23	1.2±0.4
	3-Jul	22.20	3	9.14	1.11	1.40	2.9	272	3.9	284	23.2	-10.6	113±51	152±46	1.3±1.4
	3-Aug	21.50	5.5	9.57	1.14	1.44	2.9	274	4.4	224	19.2	-9.5	216±5	369±14	1.7±0.1
	10-Sep	17.70	7	9.33	1.01	1.23	3.2	281	5.6	209	20.5	-9.2	98±24	179±23	1.8±0.4
	26-Oct	7.30	n.s.	10.48	0.91	1.20	3.2	271	5.8	280	24.0	-9.7	164±60	108±44	0.7±0.4
D'argent	27-May	15.87	3.5	10.10	1.05	4.08	8.2	26			21.6	-12.1	155±22	237±21	1.5±0.3
	22-Jul	22.00	3	8.88	1.05	4.11	8.5	26			21.9	-11.6	299±24	344±21	1.1±0.1
	2-Nov	7.50	n.s.	10.56	0.90	4.10	9.6	26			24.4	-11.0	61±33	24±31	0.4±0.5
Bowker	27-May	12.00	3.5	11.24	1.07	0.85	3.1	18			23.8	-9.9	70±22	71±16	1.0±0.7
	22-Jul	21.00	7	9.36	1.09	1.09		32			23.8	-9.7	123±17	101±14	0.8±0.3
	2-Nov	8.60	n.s.	10.97	0.96	0.97	2.5	25			24.1	-9.4	94±25	63±18	0.7±0.3
Brome	28-May	15.02	8	11.26	1.16	24.69	3.8	35			21.1	-11.1	686±17	550±25	0.8±0.1
	23-Jul	22.10	6	8.77	1.04	4.17	3.6	35			21.8	-10.5	424±30	368±28	0.9±0.1
	3-Nov	8.10	n.s.	10.89	0.94	14.43	4.7	35			24.3	-9.8	192±51	118±41	0.6±0.3
Orford	27-May	13.67	5	10.99	1.09	1.16	3.6	47			22.7	-10.1	160±33	171±33	1.1±0.4
	22-Jul	22.00	6	9.57	1.14	2.21		49			21.7	-9.7	206±63	238±52	1.2±0.6

	2-Nov	8.40	n.s.	10.93	0.95	1.69	4.3	48	24.2	-9.3	162±18	106±14	0.7±0.1
Waterloo	28-May	15.77	4	9.14	0.96	7.83	10.1	46	21.4	-11.9	473±26	431±25	0.9±0.1
	23-Jul	22.70	4	8.85	1.06	18.87	6.2	46	24.0	-9.9	866±29	582±32	0.7±0.1
	3-Nov	7.20	4	9.61	0.81	13.35	3.9	46	24.2	-10.1	164±35	81±46	0.5±0.3
la Peche	3-Jun	14.65	7	10.25	1.02	3.55		30	22.7	-9.1	342±19	279±20	0.8±0.1
	25-Jul	22.40	5	9.72	1.13	3.40	4.4	30	23.0	-9.1	406±21	341±24	0.8±0.1
	31-Oct	9.00	n.s.	9.57	0.84	3.48	3.7	30	24.1	-9.5	131±35	81±36	0.6±0.3
Phillippe	3-Jun	14.90	6	10.57	1.06	1.76	7.7	21	23.5	-9.8	308±22	230±22	0.7±0.1
	25-Jul	21.90	5	9.28	1.07	1.75		21	21.3	-9.3	222±30	285±27	1.3±0.2
	31-Oct	9.10	n.s.	10.07	0.88	1.75	5.8	21	24.3	-8.8	92±43	51±53	0.6±0.6

n.s. not stratified.
* indicates oxygen concentrations measured in the lab with Winkler method.

Planktonic production in the epilimnion (GPP) was calculated from R, $[O_2]$, and $\delta^{18}O_{DO}$ according to the $\delta^{18}O$ method in Chapter 1 and the parameters used for this calculation are shown in Table 2-2. GPP ranged from 16 to 749 mg O_2 m^{-3} d^{-1} and averaged 212±30 mg O_2 m^{-3} d^{-1}. GPP was also lowest in October and highest in mid-summer. Average GPP during the stratified season for the four Laurentian lakes that were previously studied by Carignan et al. (2000) were not significantly different from earlier results. However, our measures of GPP for the Eastern Township lakes were widely different from those reported by del Giorgio et al. (1994). Our measures of production in lakes Bowker, Argent and Orford, the more oligotrophic of the Township Lakes, were 2 to 3 times greater, sixty percent greater for Lake Brome and about fifty percent less for Lake Waterloo, the most eutrophic lake.

A two way ANOVA was performed on GPP from the Laurentian lakes that were sampled on a montly basis and showed that GPP varies significantly with time ($p<0.001$, $df=13$) and with lake sampled ($p<0.001$, $df=5$). Analysis of variance of GPP for the twenty one lakes sampled in May, July and October also showed that GPP varies significantly with time ($p<0.001$, $df=20$) and with lake sampled ($p<0.001$, $df=2$).To examine the underlying cause for the variation in production, a stepwise multiple linear regression was performed including the physical and chemical variables. To assure consistency, October cases, when the lakes were not stratified, were not included. Nitrogen and phosphorus were not included as data was missing for a large number of the lakes. Stepwise linear regression with production as the dependent variable showed that production was a function of temperature, chlorophyll *a* and lake area (Model 1, Table 2-3) explaining about 64% of the variation in production. Temperature alone explained 30% of the variability in production (Figure 2-2a).

GPP increases with increasing dissolved organic carbon (Model 2). The stepwise multiple regression was performed a second time for the Laurentian lakes where TN, TP and light extinction data was available. There was no significant relationship between GPP and TN or GPP and light extinction but GPP and TP were positively correlated (Model 3).

Volumetric GPP increased significantly as mean depth of the lake decreased (Figure 2-2b, Model 4); production was higher in shallower lakes. This is perhaps unsurprising as T, Chl-a, PAR, and TP, parameters found to be positively correlated with production, increase with decreasing lake depth.

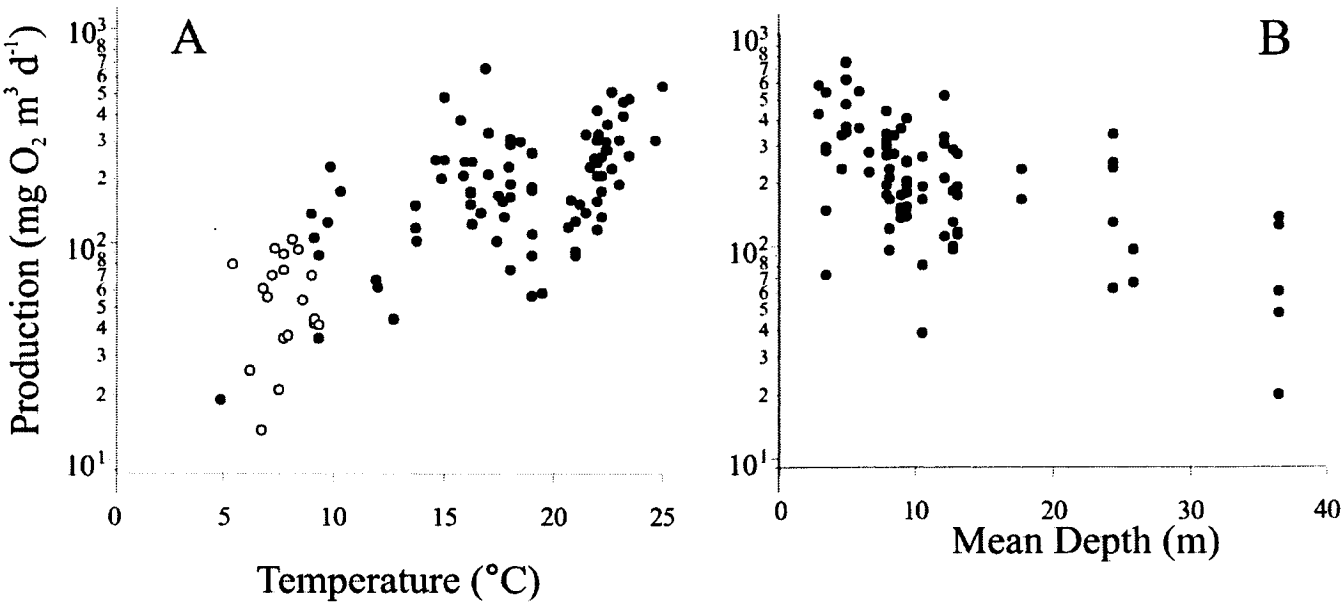

Figure 2-2. Epilimnetic production as a function of temperature (A) and mean depth (B) for the twenty-one lakes sampled during the stratified period of 2003. Open circles indicate measurements from the unstratified period.

Table 2-3. Linear regression models relating metabolic parameters to physical and chemical parameters, production and respiration (GPP, R, mg O_2 m^{-3} d^{-1}), temperature (T, °C), chlorophyll a (Chl-a,), alkalinity (alk, mg L^{-1}), mean depth (Z_m, m), dissolved organic carbon (DOC, mg L^{-1}), total phosphorous (TP, µmol L^{-1}), lake area (LA, km^2) and photosynthetically available radiation (PAR, µE m^{-2} min^{-1}). Models were bootstrapped 1000 times and the standard error reported with coefficients and intercepts. Condfidence intervals are shown at the α=0.05 critical level.

Model	Dependant Variable	Regression	r^2	p
1	log **GPP**	0.84±0.15 log **T** + 0.53±0.64 log **Chl-a** -0.14±0.04 log **LA** + 0.37±0.13	0.64	<0.001
2	log **GPP**	0.58±0.15 log **DOC** + 1.97±0.10	0.14	<0.001
3*	log **GPP**	0.98±0.15 log **TP** + 1.56±0.14	0.30	<0.001
4	log **GPP**	-0.51±0.10 log Z_m + 2.90±0.10	0.31	<0.001
5	log **R**	0.92±0.05 log **GPP** + 0.14**±0.12	0.79	<0.001
6	log **R**	2.06±0.60 log **T** + 0.67±0.10 log **Chl-a** + 0.33±0.15 log **PAR** + 0.13**±1.41	0.59	<0.001
7	log **R**	-0.56±0.14 log Z_m + 2.81±0.14	0.21	<0.001
8	log **R**	0.48±0.13 log **DOC** + 4.54±0.20	0.08	<0.01
9**	log **R**	0.85±0.22 log **TP** + 3.65±0.42	0.17	<0.001
10	log **GPP:R**	-0.73±0.31 log **T** - 0.64±0.14 log **Chl-a** - 0.27±0.06 log **alk** – 4.23±1.06	0.36	<0.001
11	log **GPP:R**	-0.11±0.30 log **TP** + 0.82±0.23	0.16	<0.001
12**	log **GPP:R**	-0.33±0.11 log **TP** + 1.06±0.19	0.11	<0.010

*indicates model for only the Laurentain lakes with TP data (*df*=58)

**indicates parameters not significant at the α=0.05 level.

Planktonic Respiration –

Planktonic respiration, R, ranged from 7 to 866 mg O_2 m^{-3} d^{-1} and averaged 200±55 mg O_2 m^{-3} d^{-1}. Additional data can be found in Appendix 4. R was in general lowest in October and highest in mid-summer (Table 2-2). Respiration rates measured in this study for lakes in the Eastern Townships were similar to results reported by del Giorgio et al. (1994) with the exception of Lake Bowker, where our mid-summer value was about half of their average summer measure. Four of the lakes sampled in this study were the same as lakes studied by Carignan et al. (2000) and of these there was no significant difference in the respiration rates measured. Analysis of variance showed that respiration varies significantly with time ($p<0.01$, $df=65$, and $p<0.05$, $df=39$) and with lake sampled ($p<0.001$, $df=64$, $p<0.01$, $df=39$) during the stratified period.

Planktonic production explained about 80% of the variability in planktonic respiration (Model 5). The slope of the relationship between R and GPP during the stratified period was significantly less than 1 (0.92, $p<0.001$) and its intercept (0.14±0.12 mg O_2 m^3 d^{-1}) was not significantly different from 0 ($p=0.61$), indicating that in situ production fuels planktonic respiration in the epilimnion.

Stepwise multiple regression with respiration as the dependent variable showed respiration, like production, was dependent on temperature, Chl-a and PAR (Figure 2-3a, Model 6, Table 2-3). About 20 % of the variability in respiration could be explained by variation in mean depth of the lake (Figure 2-3b, Model 7); as lake depth decreases volumetric respiration rates increase. The relationship between respiration and DOC was significant (Model 8) but DOC only explained about 8% of the variability in R. The stepwise multiple regression was performed a second time for the Laurentian lakes where TP

and TN data was available. There was no significant relationship between R and TN but R increases with increasing TP (Model 9).

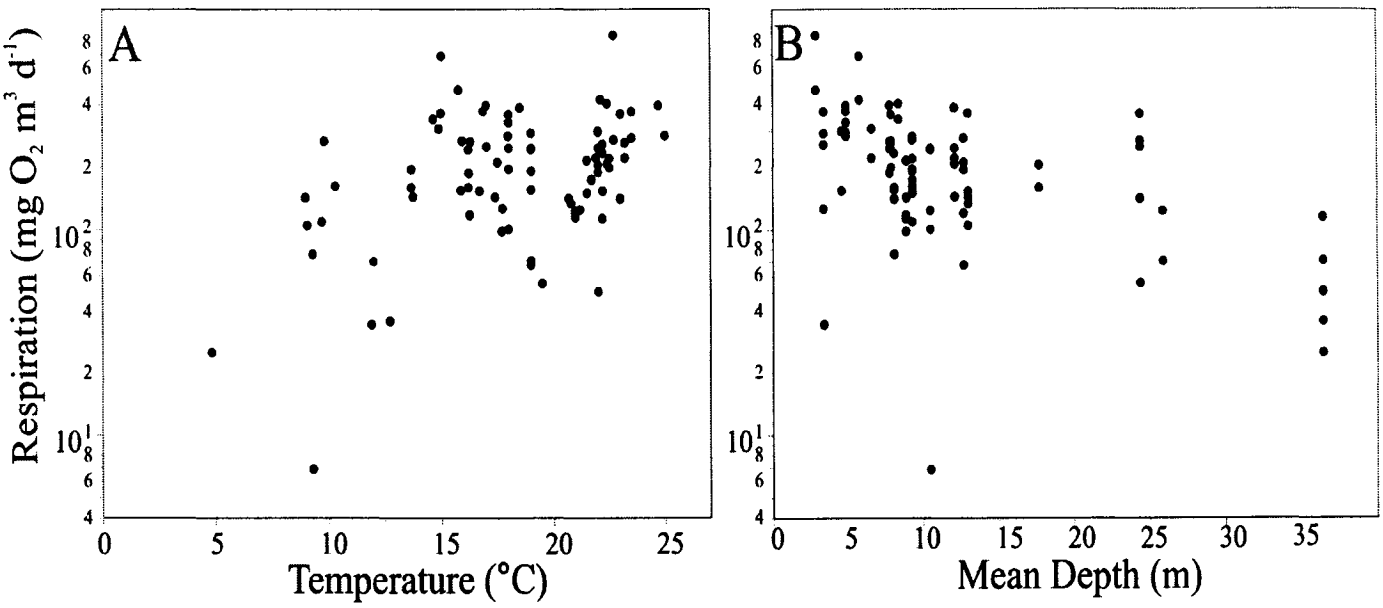

Figure 2-3. Respiration versus temperature (A) and mean depth (B) of the twenty-one lakes sampled over the stratified period of 2003.

Metabolic balance –

Mean GPP:R was 1.12±0.13 and planktonic production significantly exceeded respiration in 20% of cases, while planktonic R was significantly greater than production in only 8% of cases (Figure 2-4, n=103). However, GPP never exceeded R in October. This is perhaps unsurprising as all lakes sampled were unstratified in October and thus GPP and R were measured through the entire water column, often deeper than the photic zone of the lakes. Also, the amount of light available in October was also considerably less than during the stratified period. During the stratified season, GPP:R averaged 1.23±0.14.

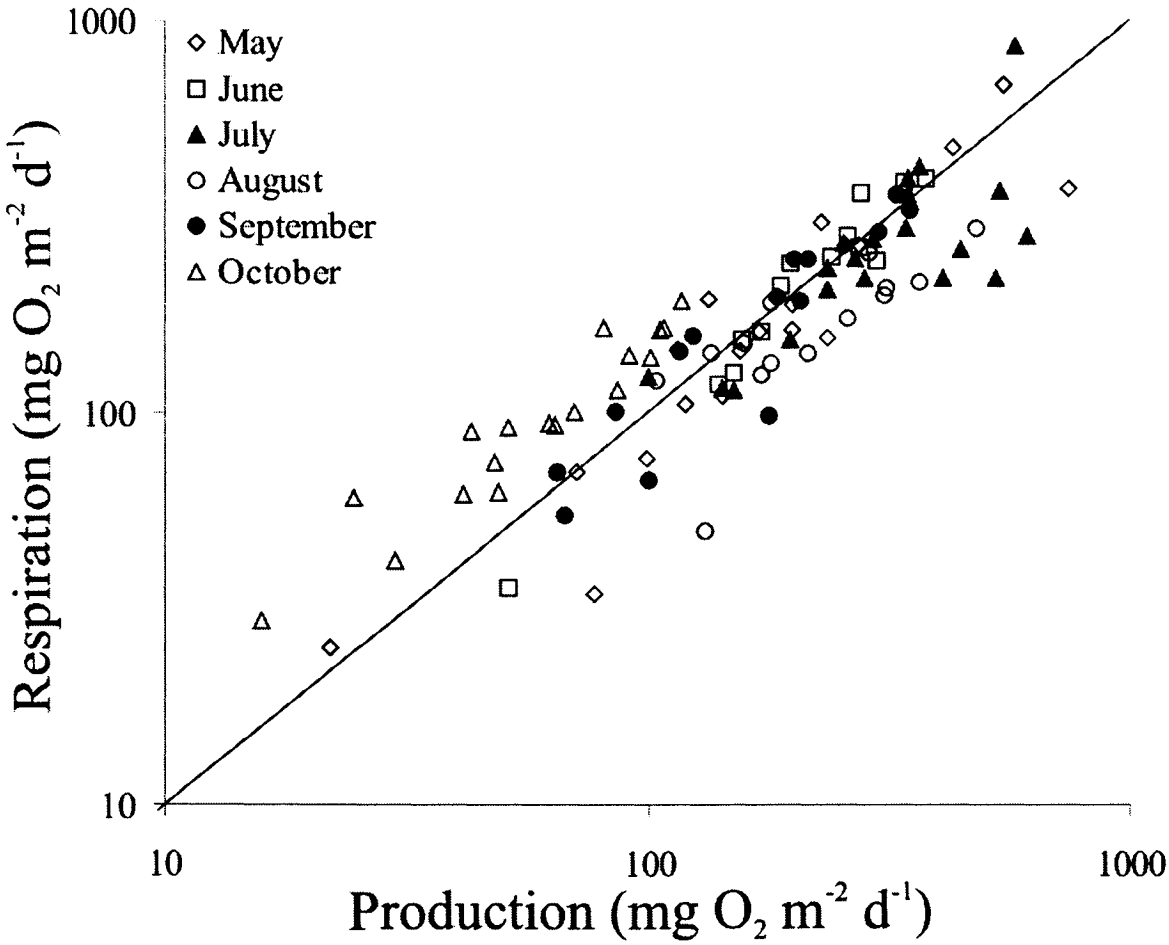

Figure 2-4. Relationship between respiration and production in twenty-one lakes sampled between May and October of 2003, plotted on a log scale. The solid line represents equal production and respiration rates.

Two way ANOVAs were performed to determine if there was significant variation in the $\delta^{18}O$ metabolic balance over time and between lakes. For the Laurentian lakes samped on a monthly basis GPP:R varied signicantly over time (p=0.005, df=5) but not between lakes (p=0.62, df=13, Figure 2-5). For the 21 lakes sampled in May, July and October, GPP:R also varied signicantly over time (p=0.003, df=2) but not between lakes (p=0.40, df=20). Thus, changes in GPP:R may be controlled by variables that change over time. A stepwise linear regression in both directions gave a linear model dependent on temperature,

chlorophyll-a and alkalinity (Model 10). Increasing temperatures cause production rates to increase more rapidly than respiration rates so that GPP:R is positively correlated to T (Figure 2-6). For the Laurentian lakes, where TP data was available, GPP:R was negatively related to TP (Model 11).

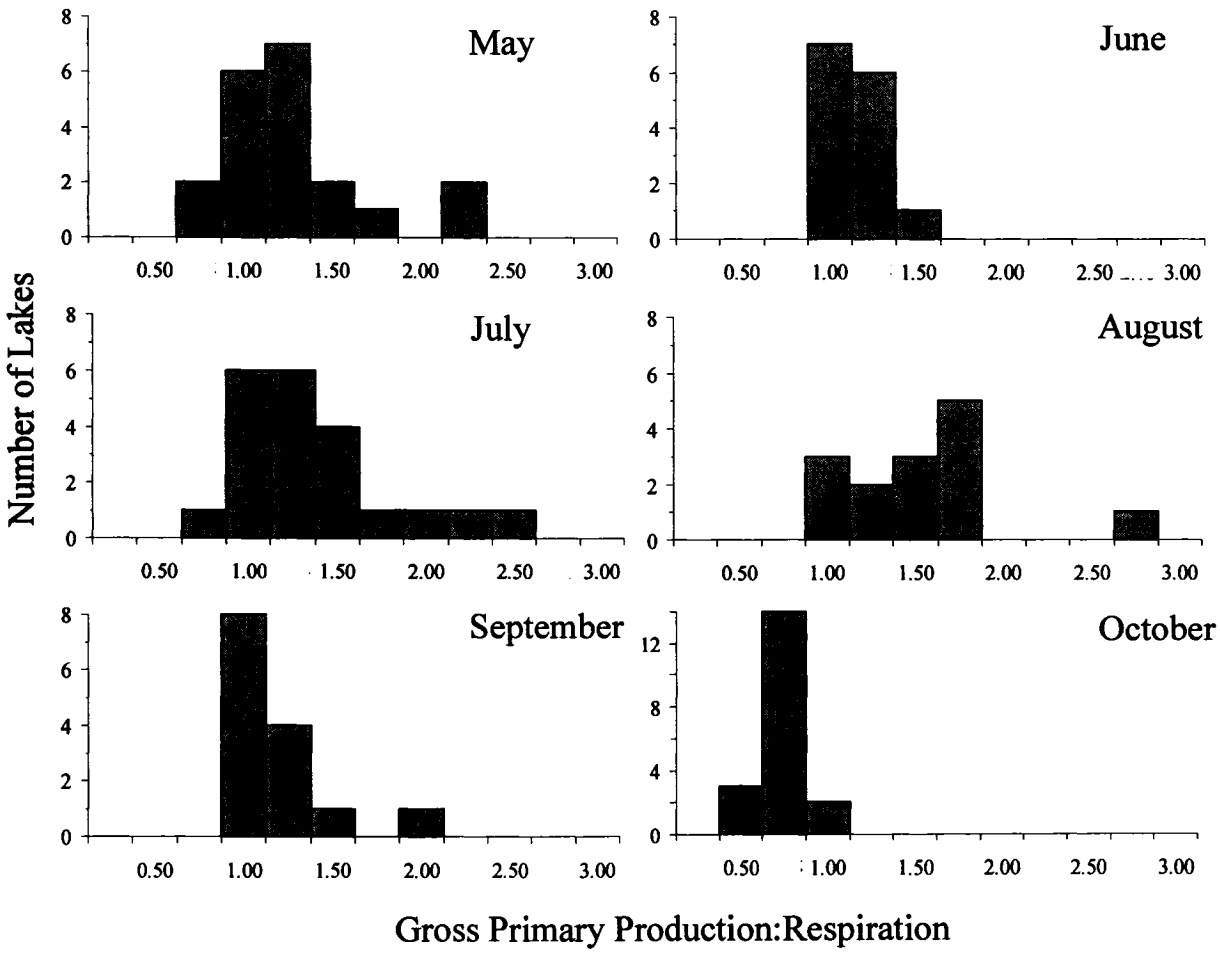

Figure 2-5. Planktonic metabolic balance (GPP:R) of the study lakes (note that n=21 for May, July and October and 14 for June, August and September).

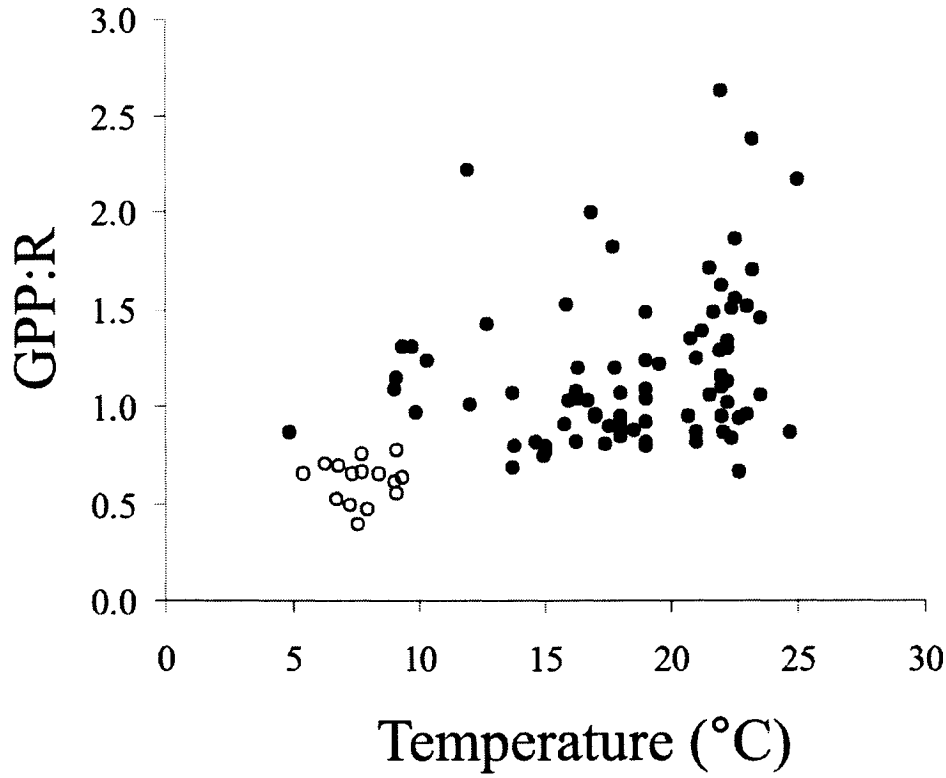

Figure 2-6. Gross primary production:respiration versus temperature of the twenty-one lakes sampled over the stratified period of 2003. Closed circles indicate measurements taken when lakes were stratified while open circles indicate measurements taken during the unstratified period.

There was no significant relationship between linear or log-linear planktonic GPP:R and DOC. For the Laurentian lakes, where TP and TN data was available, there was no significant relationship between TN and GPP:R. However, planktonic GPP:R decreased significantly with increasing TP (Model 11). Respiration rates increased more rapidly with increasing TP than production rates.

Analysis of variance shows that differences in the metabolic balance between regions were not significant in May, July or October.

Discussion

Metabolic Balance –

While several recent studies have concluded that oligotrophic northern temperate lakes are generally net heterotrophic during the summer period (del Giorgio et al. 1997; Duarte and Agustí 1998), our results provide evidence that net heterotrophy is not a universal phenomenon. The average metabolic balance of the lakes as estimated from both isotopic methods was significantly production dominated. The epilimnia of the lakes were generally oversaturated with respect to oxygen and the isotopic composition of the dissolved oxygen was less than atmospheric, indicating production dominance.

Further evidence for net autotrophy in the mixed layer comes from metalimnetic oxygen profiles. Once a lake stratifies the metalimnion can be considered closed to imports and exports of oxygen, as diffusion is a slow process. Any change in the concentration of oxygen is due to respiration or production. Of the twenty-one lakes sampled, fourteen exhibited oxygen oversaturation below the thermocline, indicating that production was greater than respiration in the metalimnion.

Oxygen saturation in the lakes we sampled averaged 104% during the stratified period. A total of twenty-four percent of the cases showed undersaturation with respect to oxygen, though only eight percent during the stratified period. Prairie et al. (2002) reported that seventy-five percent of the lakes they sampled were undersaturated in oxygen, though they do not report confirming their O_2 probe measurements with Winkler titrations. Of the lakes we sampled in the same Eastern Township region, we found undersaturation in only 10% of the cases during the stratified season. To confirm that this discrepancy was not an instrumental problem, our results of the in situ probe measurements were checked against Winkler titrations. The average difference in oxygen concentration between the two methods

was only 0.01 mg L^{-1}, showing that instrumental errors were not the cause of the discrepancy. It should be noted, however, that of the five lakes we sampled in the Eastern Townships, only Lake Bowker was included in the study by Prairie et al. and both studies found this lake to be on average oversaturated in oxygen.

While Prairie et al. (2002) did find the Eastern Township lakes to be on average net heterotrophic, they found that the degree of oxygen overstaturation, from which they implied metabolic balance, increased with decreasing trophic status. The more oligotrophic lakes were more likely to be net autotrophic. Cole et al. (2000) found both R and GPP to be positively correlated with TP, while NEP and TP were not significantly correlated. Our study found similarly that R and GPP were positively correlated with TP (n=60, r=0.45, p<0.001, r=0.55, p<0.001) though we, like Prairie et al., found pelagic GPP:R was significantly negatively correlated to TP (n=60, r=-0.40, p<0.001). Decreasing concentrations of nutrients did not result in net-heterotrophy during summer stratification.

Production rates measured in the Eastern Township lakes in this study and ten years prior by del Giorgio et al. (1994) are widely different. Ten years, of course, could account for some changes in the lake ecosystems but the concentrations of DOC and Chl-a are not significantly different between the two studies and do not support this idea. The lakes were also sampled over the same depth of mixed layer to within 0.5 m. Interannual variability in the amount of solar radiation received by the lake may influence the amount of production in the lakes. Yet, it is unlikely that a small difference in PAR could account for the magnitude of the difference in production estimates.

For the Gatineau lakes, it is a near certainty that the methodological differences result in the difference between Wang and Veizer (2000, 2004) and our results. The method used

in the earlier study to estimate P:R is undefined when oxygen concentrations are near saturation and will provide erroneous results under these circumstances.

Dissolved Organic Carbon –

Prairie et al. (2002) found that lakes are net-autotrophic when concentrations of dissolved organic carbon are below 4 and 6 mg L^{-1} and net-heterotrophic when DOC concentrations are above 4 to 6 mg L^{-1}. The lakes sampled in our study span this range of DOC concentration (1.9 to 15.1 mg L^{-1}, though approximately 55% are below the threshold). We found that both planktonic R and GPP increased with increasing DOC but that neither $\delta^{18}O$ nor $\delta^{13}C$ GPP:R estimates showed a significant correlation with DOC. When the cases were grouped into below, within, and above the DOC threshold proposed by Prairie et al., there was no significant correlations between DOC and GPP:R. Furthermore, the pelagic metabolic balance of the lakes within the threshold range was significantly greater than equilibrium (1.34±0.18, p=0.05) and not different from lakes with DOC concentrations below 4.0 mg L^{-1} (1.31±0.12). However, the average metabolic balance of lakes with DOC concentrations above 6 mg L^{-1}, was less, 1.16±0.13 (though still not significantly less at the α=0.05 critical level). Likewise, lakes with DOC concentrations above 6 mg L^{-1} were less oversaturated with respect to oxygen than lakes with lower DOC levels. All lakes which showed metalimnetic oxygen peaks in mid-summer had DOC concentrations below 5 mg L^{-1} while 6 of the 7 lakes that did not show oxygen supersaturation in the metalimnion had DOC concentration over 5 mg L^{-1}. This suggests that high DOC levels do not allow sufficient light for metalimnetic production and in lakes with concentrations of DOC over 5 mg L^{-1} respiration will exceed production in the metalimnion. Nevertheless, our results do not

support the hypothesis that DOC concentrations over 5 or 6 mg L^{-1} in the epilimnion cause net heterotropy.

Jannson et al. (2000) found a negative exponential relationship between net autotrophy and DOC levels. Their threshold between net heterotrophy and net autotrophy was higher than that of Prairie et al. (2002), approximately 10 mg L^{-1}. Only three of the cases we sampled had DOC concentrations over 10 mg L^{-1} making it difficult to assess this idea, yet our data did agree that net heterotrophy occurs at concentrations of DOC above 10 mg L^{-1}. Hanson et al. (2003) measured GPP and R from changes in oxygen and carbon dioxide concentrations in 25 lakes in Wisconsin and Michigan with a wide range of DOC concentrations. This method cannot be expected to give identical results to bottle incubations or to oxygen isotope methods as it completely includes the respiration flux of the littoral sediments. However, they also found that lakes tended towards net heterotrophy when DOC concentrations were above 10 mg L^{-1} and that lakes were closer to metabolic equilibrium at lower concentrations of DOC, again disputing the idea that unproductive ecosystems are respiration dominated.

Physical parameters and metabolic balance –

Weather conditions influence the metabolic balance of the lakes. We found that there was no statistically significant difference between the metabolic balance of the lakes over the stratified season though GPP:R changed over time. While mid-summer was strongly autotrophic, late October was strongly heterotrophic. Temperature was the strongest influence on GPP:R. Temperature parameters affect not only the metabolism of phytoplankton and bacteria but also affect the depth of the mixed layer.

While the lakes studied were net autotrophic during the stratified period, they were net heterotrophic when sampled in October. Our results reported for October samples apply

to the entire water column, as the lakes were destratified. There are several probable causes for this change from net autotrophy to net heterotrophy. Unlike the stratified period, a considerable portion of the water column sampled was below the photic zone in October. Secondly, the amount of solar radiation available for phytoplankton is markedly less in October than mid-summer. Also, as the mixed layer thickens more of the lakes sediments are in contact with the mixed layer. The metabolic processes occurring in these sediments consume oxygen and will be partially responsible for the degree of oxygen undersaturation seen in October. Finally, the hypolimnia of many of the lakes became severely undersaturated in oxygen over the stratified period, resulting in a reducing environment. A downward progression of the thermocline not only mixes the oversaturated water in the epilimnion with the anoxic water of the hypolimnion but also exposes reduced carbon in the hypolimnion to chemical and biological oxygenation, which is incorporated into our measure of respiration from both isotopic methods.

Conclusions

Multiple lines of evidence demonstrate that net heterotrophy is not a general occurrence in northern temperate lakes. Firstly, the epilimnia of the study lakes were frequently oversaturated in oxygen during the summer months and the isotopic composition of the dissolved oxygen provides evidence that production dominance was a likely source of the oxygen oversaturation. Secondly, the slope of the relationship between planktonic R and GPP was significantly less than 1 and its intercept was not significantly different than 0, indicating that planktonic GPP fuels planktonic R. Thirdly, GPP:R as measured with the $\delta^{18}O$ method found GPP was on average greater than R during the ice-free season. Finally, more than half of the lakes sampled developed metalimnetic oxygen peaks during the

summer months: a phenomenon that could only occur if GPP was greater than R even below the thermocline.

GPP, R, and the balance between GPP and R were all most strongly correlated with lake temperature, which in turn is a function of the amount of solar radiation received by the lake. Our results imply that it is this solar radiation that drives planktonic gross primary productivity, which in turn drives the majority of planktonic respiration. Variation in DOC only explained 8% of the variation in planktonic R, while variation in planktonic GPP explained approximately 80% of the variation in planktonic R.

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Chapter 3 Carbon dioxide oversaturation in lake waters; examining plausible causes

Abstract

Lakes worldwide are commonly oversaturated with carbon dioxide, however the source of this CO_2 oversaturation is not well understood. A study of carbon dynamics in 23 Quebec lakes was carried out to measure the magnitude of the carbon flux to the atmosphere and to examine the underlying cause for carbon dioxide oversaturation. Atmospheric carbon dioxide flux, gross primary production (GPP), community respiration (R) and the isotopic composition of dissolved inorganic carbon were measured. All of the lakes sampled were oversaturated with carbon dioxide over the sampling period, on average 252 ± 25%. However, we found little evidence to conclude this carbon dioxide oversaturation was the result of an excess of in situ respiration over in situ production. The annual excess of R over GPP was not sufficient to account for the size of the CO_2 flux to the atmosphere; average annual GPP –R was –7.7 ± 5.6 mg C m^{-2} d^{-1} while the average annual flux of CO_2 to the atmosphere was 45 mg C m^{-2} d^{-1}. Carbon evasion was not a function of respiratory flux, nor did the isotopic signature of dissolved CO_2 in the lakes present evidence of excess R over GPP.

Introduction

Lake, rivers and streams worldwide are commonly oversaturated with respect to atmospheric carbon dioxide resulting in a net flux of CO_2 from freshwater aquatic systems (e.g. Kling et al. 1991, Cole et al. 1994, Sobek et al. 2005). Cole et al. (1994) analyzed data on the partial pressure of carbon dioxide in the surface waters of 1835 lakes distributed worldwide and found that 87% were supersaturated in CO_2. Sobek et al. (2005) analysed data from 4902 lakes and found 93% were oversaturated in CO_2 with respect to the

atmosphere. Despite this general phenomenon, the source of CO_2 oversaturation is not well documented.

Several processes control the concentration of CO_2 in an aquatic ecosystem: respiration, primary production, exchange with the atmosphere, and external inputs and outputs such as streams, overland flow and groundwater. Carbon dioxide oversaturation is often presented as evidence of an excess of in-lake respiration over in-lake primary production (del Giorgio and Peters 1994, Hanson et al. 2003, Sobek et al. 2003) but this may not be the major source of inorganic carbon. The metabolic balance of lakes has been a highly debated subject for many years and, while some studies have found that respiration exceeds production in all but the most eutrophic ecosystems (del Giorgio and Peters 1994), others have observed that production exceeds respiration even in oligotrophic lakes that were oversaturated with CO_2 (Carignan et al. 2000). Riera et al. (1999) and Jonsson et al. (2003) found that even when lakes were net heterotrophic, production of CO_2 by respiration could not account for the degree of carbon dioxide oversaturation.

The role of northern forest biomes in the global carbon cycle has been a subject of intense debate for the last ten years since Ciais et al. (1995) proposed the existence of a large terrestrial biospheric sink of CO_2 in the temperate latitudes of the Northern Hemisphere. Forest inventory data from temperate and boreal biomes suggests that about half of the "missing carbon sink" is in these forests (Liski et al. 2003). However, such inventories do not take into account the transport of carbon from forests to aquatic systems. If the source of carbon dioxide oversaturation in lakes is from forest ecosystems, then these models overestimate the magnitude of the proposed sink.

Stable isotopes of carbon can be used as tracers of CO_2 in the aquatic system. In the northern hemisphere atmospheric CO_2 has a $\delta^{13}C$ value around –8 ‰ VPDB. Dissolution

and gas transfer into water are both isotopically fractionating processes, yielding $\delta^{13}C$ values near –11‰ for dissolved CO_2 (Zhang et al. 1995) (Figure 3-1). Aquatic photosynthesis preferentially consumes ^{12}C, leaving the residual carbon dioxide pool enriched in ^{13}C (Baird et al. 2001) with the magnitude of the enrichment depending on the amount of CO_2 available to photosynthesizing organisms. As a result, the organic matter produced by aquatic photosynthesis is isotopically depleted, with a $\delta^{13}C$ value approximately 20‰ lighter than the isotopic composition of the dissolved CO_2 (Leggett et al. 1999). The competing process, in situ respiration, consumes this depleted organic matter and produces CO_2 with a similarly depleted isotopic composition (Keough et al. 1998).

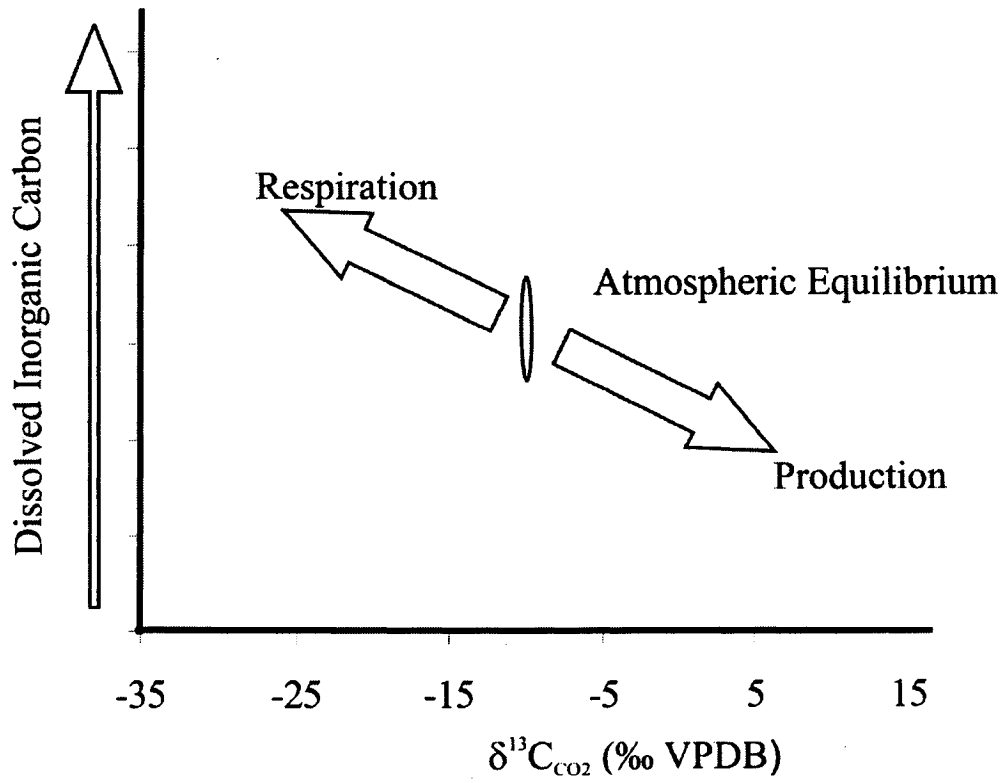

Figure 3-1. Effect of atmospheric exchange, photosynthesis and respiration on the isotopic composition of dissolved CO_2 and the concentration of dissolved inorganic carbon.

The isotopic compositions of terrestrial carbon inputs vary with the source of carbon. The isotopic value of soil CO_2 that originates from decomposition of terrestrial organic matter dominated by C3 plants averages about –27‰ (Vogel 1993). Mineralization of this organic carbon imparts little isotopic fractionation, but the steep CO_2 concentration gradient between soil and air can cause kinetic fractionation of about 4‰ (Cerling et al. 1991). Furthermore, dissolution of CO_2 into water is also a fractionating process (Zhang et al. 1995) so that the final $\delta^{13}C$ of CO_2 ($\delta^{13}C_{CO2}$) dissolved in soil water is about -24‰. Weathering of minerals can further change the carbon isotope value of CO_2 in groundwater. Carbonates generally have $\delta^{13}C$ values near 0‰ and their dissolution by carbonic acid in groundwater produces CO_2 with an isotopic composition that depends on the concentration of carbonic acid, its initial isotopic signature, and the degree of saturation. The resulting $\delta^{13}C_{CO2}$ is a mixture of these two sources, about –14 to –22‰ (Clark and Fritz 1997). Silicate weathering also consumes CO_2 but does not affect its isotopic value (Pawellek and Veizer 1994). Photooxidation of dissolved organic matter enriches the dissolved organic carbon (DOC) in ^{13}C and thereby increases the ration of ^{12}C to ^{13}C the dissolved CO_2 pool (Osburn et al. 2001). Methanogenesis preferentially consumes the light isotope of dissolved CO_2 and thereby enriches the dissolved inorganic carbon (DIC) pool in ^{13}C (Hornibrook et al. 2000).

Twenty-three lakes in three regions of Quebec were sampled between 2002 and 2003 and the isotopic composition of dissolved carbon dioxide was used in an attempt to discern the source of carbon dioxide oversaturation.

Methods

Study Site -

To examine temporal changes of carbon dynamics in the lakes, we sampled two lakes in the Laurentian region of Quebec, approximately 70 km northwest of Montreal on the Canadian Shield, on a weekly basis between May 2002 and March 2003. Lac Croche is a small, oligotrophic, clearwater lake with virtually no macrophytes, low DOC and TP while Lac à l'Ours is a mesotrophic lake with higher concentrations of dissolved organic carbon and phosphorous due to its high drainage ratio and the presence of wetlands in its watershed (Table 3-1).

In an attempt to examine spatial changes in lake carbon dynamics, we also sampled twenty-one lakes in three regions of Quebec over the ice-free season of 2003. We sampled fourteen lakes in the Laurentians, between 60 and 120 km northwest of Montreal on the Canadian Shield, on a monthly basis during the ice-free season of 2003. The area is underlain primarily by silicate bedrock covered by 1-5m of glacial till. Five lakes in the Eastern Townships, south of Montreal, were sampled in the spring, summer and fall of 2003. While some of these lakes sit on the sedimentary rocks of the St. Lawrence lowlands, metamorphic shists underlie others. Three of the lakes sampled were strongly stratified while Lac Brome was only weakly stratified, and Lac Waterloo did not stratify. We also sampled two lakes in the Gatineau hills of Quebec, north of Ottawa, in the spring, summer and fall of 2003. These lakes are also on the Canadian Shield and are underlain primarily by granites and marbles.

Table 3-1. Morphometric properties of the 23 study lakes. *n* = number of times sampled, LA= lake area (km^2) WA = watershed area (km^2), *Zm* = mean depth (m).

Lake	Region	Location	*n*	LA	WA	*Zm*
Achigan	Laurentians	45°56'N, 74°00'W	6	5.31	96.5	12.7
d'Argent	Eastern Townships	45°29'N, 72°28'W	3	1.00	13.2	4.6
de la Blanche	Laurentians	46°08'N, 74°44'W	6	0.41	1.14	10.5
Bowker	Eastern Townships	45°42'N, 72°21'W	3	2.30	8.10	25.9
Brome	Eastern Townships	45°23'N, 72°49'W	3	14.5	185.7	5.8
Connelly	Laurentians	45°53'N, 73°58'W	5	1.24	24.4	7.8
En Coeur	Laurentians	45°58'N, 74°01'W	5	0.47	1.6	3.4
Gervais	Laurentians	46°16'N, 74°41'W	6	0.97	8.8	24.4
La Pêche	Gatineau	45°59'N, 75°98'W	3	7.05	93.8	8.4
Montange Noire	Laurentians	46°12'N, 74°16'W	6	2.80	12.6	13.0
du Nord	Laurentians	46°03'N, 74°02'W	6	4.02	34.9	7.9
Orford	Eastern Townships	45°29'N, 72°27'W	3	1.30	10.6	17.7
Ouimet	Laurentians	46°10'N, 74°35'W	6	1.60	16.7	9.3
Phillippe	Gatineau	45°63'N, 76°18'W	3	1.72	18.4	6.6
Pin Rouge	Laurentians	45°57'N, 74°02'W	6	0.15	7.00	4.9
de la Rouge	Laurentians	46°07'N, 74°42'W	6	0.66	3.45	8.1
des Sables	Laurentians	46°01'N, 74°15'W	6	2.92	35.4	9.3
St. Joseph	Laurentians	45°96'N, 74°33'W	6	1.47	14.9	12.1
Tremblant	Laurentians	46°12'N, 74°35'W	6	9.56	129.3	36.5
à la Truite	Laurentians	46°01'N, 74°15'W	6	0.49	1.04	8.9
à l'Ours	Laurentians	45°58'N, 74°01'W	40	0.15	3.26	6.7
Croche	Laurentians	45°58'N, 74°01'W	40	0.19	0.88	5.1
Waterloo	Eastern Townships	45°27'N, 74°68'W	3	1.50	31.6	2.9

Sampling Procedures -

Between May 2002 and March 2003, we sampled lakes Croche and à l'Ours on a weekly basis, excluding two weeks in November when the lakes were not yet completely frozen. Water was collected with a 4 L Van Dorn Bottle between 07h00 and 10h00. Morning sampling ensured the epilimnion was completely mixed during the summer stratification period. Throughout this report, the epilimnion is defined as the surface mixed layer where the vertical temperature gradient does not exceed 1°C m^{-1}. Water for isotopic analysis was collected on a weekly basis from the mixed layer in 40 mL amber glass bottles with silicon/teflon septa for carbon isotopes and in a 10 mL Exetainer (VWR) with a rubber septa for dissolved oxygen isotope analysis. In order to assure their suitability for $\delta^{13}C$, these samples were poisoned with $HgCl_2$, refrigerated at 4°C and analyzed within a maximum of four months after collection.

Oxygen and temperature profiles were measured at half-meter intervals with a YSI Model 55 instrument, equipped with a stirrer. The probe was calibrated before each use in vapour-saturated air with respect to atmospheric pressure at the same temperature as the epilimnion water. The degree of oxygen saturation was calculated with respect to temperature and pressure according to Benson and Krause (1984). Alkalinity, pH and total dissolved solids (TDS) were measured for each isotope sample in the field with a Hach field chemistry kit (Loveland, CO). The light extinction coefficient of the water column was measured (Li-Cor LI-192 and LI-190 sensors) at half-meter intervals. The amount of photosynthetically available radiation (PAR) was measured (Li-Cor LI-190) at Lac Croche and these values were used to estimate PAR at the nearby lakes. Chlorophyll was measured by spectrophotometery after overnight extraction of frozen GF/C filters in cold ethanol

(Sartorg and Grobbelaar 1984) and corrected for phaeopigments. Carbon dioxide concentrations were measured at one-meter intervals throughout the water column. Samples were taken in 60 mL syringes, transported to the lab and their temperature allowed to equilibrate with cool water. Thirty mL of sample was equilibrated with 30 mL CO_2-free gas and the carbon dioxide concentration of the resultant gas measured within one hour of sampling with a LI-COR LI-820 CO_2 analyzer. Henry's law was then used to calculate the concentration of dissolved CO_2 in the water samples

Between May and October 2003, we sampled 14 Laurentian lakes on a monthly basis and two Gatineau and five Eastern Township lakes in May, July and October. Oxygen, temperature, alkalinity, pH, TDS and stable isotopes were measured in the same manner as the 2002 samples. Dissolved inorganic carbon concentrations (DIC) were analyzed using a OI Analytical "TIC-TOC" Analyzer, concentrations of CO_2 were calculated from DIC and pH measurements and the degree of CO_2 saturation (CO_{2sat}) was then calculated with respect to temperature and pressure. CO_2 concentrations measured with this method were within 10% of measurements made with the LI-COR LI-820 CO_2 analyzer

To estimate $\delta^{13}C_{DIC}$ and the concentration of DIC of groundwater, samples were taken from wells in the watersheds of most lakes sampled. Temperature, alkalinity and pH were measured in the field and used to calculate the concentration of DIC. Samples of $\delta^{13}C_{DIC}$ were collected, stored and measured as for $\delta^{13}C_{DIC}$ in lake water. In Lac Croche, samples were taken from twelve piezometers installed throughout the watershed. Despite the spatial variation, the $\delta^{13}C_{DIC}$ of all samples was within ± 1.5‰ of the mean. In sixteen of the lakes sampled in 2003, samples were taken from domestic wells in the watersheds of the lakes on each occasion lake samples were collected. Water was flushed for several minutes

before the sample was collected to reduce the chance of equilibration with the atmosphere but, as the depth of the wells and installation materials are not known, $\delta^{13}C_{DIC}$ should be viewed as only a rough estimate of the isotopic signature of groundwater in the watershed.

Laboratory Procedures -

Community respiration (R) in the mixed layer was measured twice monthly for lakes Croche and à l'Ours and on every sampling occasion for the lakes sampled in 2003. Water was collected with a 4 L Van Dorn Bottle. Samples for respiration measurements were taken from the entire epilimnetic water column and pooled in 20 L dark polyethylene containers. The water was then distributed in quadruplicate into clear 300 mL pyrex bottles that were used for measurement of the initial concentration of dissolved oxygen. A complementary set of quadruplicate dark 300 mL pyrex bottles were placed in an incubator at in situ temperatures for 6 to 8 hours. A high precision Winkler method (Carignan et al. 1998) was used to determine community respiration (R) from changes in dissolved oxygen concentration in clear and dark bottles during the incubation. The detection limits for R was 0.5 mg C m^{-3} h^{-1}. Respiration rates were calculated assuming that respiration rates measured from water sampled in the morning were representative of the entire day.

Gross primary production (GPP) in the mixed layer was calculated from $\delta^{18}O_{DO}$, $\delta^{18}O_W$ and R according to Chapter 1. Briefly, both the concentration and isotopic composition of dissolved oxygen are a function of respiration, atmospheric exchange and production. By measuring the amount of respiration and atmospheric exchange, as well as the isotopic composition of these components, an isotope mass balance equation can be used to calculate the amount of production. Variables required for the model described in Chapter 1 include the isotopic composition of dissolved oxygen and water ($\delta^{18}O_{DO}$, $\delta^{18}O_W$),

respiration (R), temperature (T), concentration of dissolved oxygen ($[O_2]$), and depth of the mixed layer (e_z). Fractionation due to respiration (ε_r) was determined from empirical values in Chapter 1, measured extinction coefficients and measured PAR.

Samples for the isotopic composition of dissolved oxygen and water, $\delta^{18}O_{DO}$ and $\delta^{18}O_W$ were analysed as in Chapter 1. Samples for $\delta^{13}C_{DIC}$ and $\delta^{13}C_{DOC}$ were analysed at the G. G. Hatch Isotope Laboratory on an OI Analytical "TIC-TOC" Analyser following the procedure outlined by St. Jean (2003). Briefly, samples were first analysed for the concentration of organic and inorganic carbon in a TIC-TOC analyser and then a helium carrier gas was used to transport the resulting CO_2 into a Finnigan Mat DeltaPlus isotope ratio mass spectrometer for isotopic analysis by continuous flow. Standard deviation of isotope samples was ± 0.2‰.

As CO_2 dissolves in water and speciates, the $\delta^{13}C$ of the resulting DIC will be controlled by the relative concentration of each DIC species and its associated fractionation factors. Of course, the relative concentration of each DIC species is dependent on pH and thus $\delta^{13}C_{DIC}$ is not solely dependent on the isotopic composition of the source of the inorganic carbon, but is strongly affected by pH. To facilitate comparison of isotope data from lakes with different pH values, we calculated the isotopic signature of dissolved CO_2, $\delta^{13}C_{CO2}$, from $\delta^{13}C_{DIC}$, pH, and temperature according to the fractionation factors given in Zhang et al. (1995) and the temperature dependent carbon dioxide speciation equations given in Clark and Fritz (1997).

Carbon Dioxide Flux Calculations -

We estimated evasion from the lakes sampled over the ice-free season using the flux equation:

$$F = k(C_{water} - C_{equilibrium}) \quad (1)$$

where F is the evasion flux, C_{water} is the concentration of CO_2 in the water, $C_{equilibrium}$ is the concentration of dissolved CO_2 in equilibrium with atmospheric CO_2 and is dependent on temperature and pressure, and k is the gas transfer velocity. Cole and Caraco (1998) used SF_6 to measure the atmospheric exchange of carbon dioxide in a small oligotrophic lake and found that the gas transfer velocity, k, of CO_2 normalized to a Schmidt number of 600 (2.65 ± 0.12 cm h^{-1}), was independent of wind at low wind speeds. We used the temperature dependency relationships in Wanninkhof (1992) to determine appropriate Schmidt numbers and the relationship

$$k = k_{600}\left(\frac{Sc_{CO_2}}{600}\right)^{-0.50} \quad (2)$$

where Sc_{CO2} is the Schmidt number of carbon dioxide, to calculate the gas transfer velocities.

In 2003, the total flux of carbon dioxide from the lakes over the ice-free period was calculated after linearly interpolating flux estimates between sampling dates. For lakes Croche and à l'Ours, where winter samples were taken, the total annual flux of CO_2 was calculated from measurements taken during the ice free period and from differences in concentrations between late March (just before ice break-up) and mid May (before stratification).

GPP – R Calculations -

To determine whether an excess of respiration over production could account for the CO_2 flux from the lakes, we estimated the difference between gross primary production (GPP) and community respiration (R) in the whole-lake. In the mixed layer R was measured from bottle incubations and the Winkler method and GPP was measured from the $\delta^{18}O$ method described in Chapter 1. Below the mixed layer, changes in oxygen concentration are

not affected by atmospheric flux, so a decrease in $[O_2]$ over time is the result of R exceeding GPP. Weekly (for lakes Croche and à l'Ours) or monthly oxygen profiles were used to estimate the change in oxygen concentration over time at one-meter intervals in the water column. Bathymetric data was then used to calculate the volume of water in each layer and these volumes, with measurements of GPP and R from the mixed layer and from the oxygen profiles below the mixed layer, were used to calculate the difference between GPP and R in the whole-lake. A photosynthetic quotient of 1.25 (Grande 1989, but see discussion) was used to convert from oxygen units to carbon units so comparisons could be made with the CO_2 flux from the lakes. Whole-lake estimates of GPP - R were made on a weekly basis for lakes Croche and à l'Ours and on a monthly basis for the fourteen Laurentian lakes sampled in 2003. We had insufficient data to estimate whole-lake GPP - R from the Eastern Township and Gatineau lakes.

Oxygen and carbon dioxide profiles under ice-cover were measured in lakes Croche and à l'Ours and used to estimate winter GPP - R. Using a photosynthetic quotient of 1.25, estimates of GPP - R from oxygen and carbon dioxide profiles agreed within ± 10 mg C m^{-2} d^{-1}. We applied the average winter GPP - R estimates from lakes Croche and à l'Ours to the Laurentian lakes as a rough, first-order, estimate of winter GPP - R.

Carbon Mass Balance -

Bade et al. (2004) describe a process-based model that attempts to explain the flux of dissolved inorganic carbon. The change in the concentration of DIC is equal to the amount produced by respiration (R) minus the amount consumed by gross primary production (GPP) plus the amount that invades from the atmosphere, where the atmospheric component is defined as the difference between the concentration of CO_2 in water in equilibrium with the

atmosphere (CO_{2eq}) and the actual concentration of CO_2 in the water (CO_2) multiplied by the gas transfer velocity (k) over the depth of the mixed layer (Z):

$$\frac{d[DIC]}{dt} = R - GPP + \frac{k(CO_{2_{eq}} - [CO_2])}{Z} \quad (3).$$

The isotope mass balance for the carbon in the mixed layer is modeled similarly except that it accounts for the isotopic compositions of the components and fractionation due to production, gas dissolution and chemical speciation. Respiration (R) is the sum of respiration of autochthonous material (R_A) and respiration of allochthonous material (R_H):

$$R = R_A + R_H \quad (4).$$

R_A is assumed to be 90% of GPP (Cole et al. 2000) with the remaining10% assumed to be buried or permanently removed (but see discussion) and R_H is calculated as the difference between R_A and R. Net primary productivity, NPP, is calculated as the difference between GPP and R_A and thus:

$$NPP = GPP - R_A \quad (5).$$

Substituting equations (4) and (5) into equation (3) and multiplying each component by its isotopic signature gives the differential equation for the isotope mass balance:

$$\frac{d[DI^{13}C]}{dt} = R_{H13} - NPP_{13} + \frac{k(^{13}CO_{2_{eq}} - [^{13}CO_2])}{Z} \quad (6).$$

R_H has the isotopic signature of terrestrially derived DOC, -27‰ in our C3 plant dominated basins. We use a photosynthetic fractionation factor of 20‰ (Laws et al. 1995), so that NPP_{13} is multiplied by the isotopic composition of photosynthesized carbon, $\delta^{13}C_{CO2}$ plus 20‰. $^{13}CO_{2eq}$ is the concentration of $^{13}CO_2$ in equilibrium with the atmosphere, simply CO_{2eq} multiplied by the isotopic composition of dissolved atmospheric CO_2. $[^{13}CO_2]$ is the

concentration of dissolved $^{13}CO_2$ in the water, which depends on the $\delta^{13}C_{DIC}$, pH and the fractionation factors for carbonate speciation (Zhang et al. 1995).

Following Bade et al. (2004), the initial conditions of the model were set to the measured variables and the model was run until an equilibrium $\delta^{13}C_{DIC}$ was obtained. This is the predicted isotopic composition of DIC according to the conditions of the model. Bade et al. (2004) found the model to be particularly sensitive to the amount of GPP that is respired, which determines R_A, but not greatly affected by depth of the mixed layer, temperature, isotopic fractionation factors or alkalinity. If we further assume that the differences between the predicted and observed $\delta^{13}C_{DIC}$ are the result of external inputs that are not included in the model, we can estimate the amount of DIC input to the system as well as its source, whether groundwater, overland flow or another source.

Data Analysis-

All statistical tests and confidence intervals are reported at the α=0.05 critical level. The precision of metabolic and isotopic measurements are reported as ± one standard error (SE) of the mean of *n* determinations multiplied by the student t distribution (t) for *n*-1 degrees of freedom, where $SE=SD/(n)^{1/2}$ and SD is the standard deviation. Addition and subtraction errors in the calculation of R and GPP were calculated as $SE_{A\pm B}=(SE^2_A+SE^2_B)^{1/2} \cdot t_{\alpha/2}$. Variables used in multiple linear regressions were tested against the standard normal distribution with a Chi-squared goodness of fit test. Non-normal variables were normalized by log transformation and used as such in multiple regressions. For multiple linear regressions, all regression parameters were bootstrapped 1000 times to estimate standard errors.

Results

Carbon Dioxide Concentrations -

Carbon dioxide concentration profiles were measured on a weekly basis in lakes Croche and à l'Ours between May 2002 and March 2003 (Appendix 5). During the summer months the epilimnia of both lakes showed relatively constant CO_2 concentrations, slightly above atmospheric saturation. The CO_2 concentration of the hypolimnia of the lakes increased steadily over the summer months and reached a maximum in late September. As water temperatures decreased and the thermocline increased in depth, CO_2 from the hypolimnion evaded into the upper water column and atmosphere. By November the water column of both lakes had a constant CO_2 concentration with depth. Under ice cover, when evasion to the atmosphere was prohibited, CO_2 concentrations gradually increased above November concentrations. Though we have no data for the break up period, the difference in CO_2 concentrations between late March (before ice-break-up) and May (before summer stratification) show CO_2 evasion to the atmosphere. The degree of CO_2 saturation was calculated with respect to water temperature and atmospheric pressure. Both lakes were oversaturated with respect to carbon dioxide over the year and Lac à l'Ours was consistently more oversaturated than Lac Croche. The winter degree of oversaturation did not exceed summer hypolimnetic oversaturation.

Carbon Dioxide Flux-

Both lakes evaded CO_2 to the atmosphere over the entire season and rates ranged from 31 mg C m^{-2} d^{-1} to 236 mg C m^{-2} d^{-1} in Lac Croche and slightly higher in Lac à l'Ours, from 49 mg C m^{-2} d^{-1} to 426 mg C m^{-2} d^{-1}. In both lakes evasion was lowest during the summer months and gradually increased as water temperatures decreased and the thermocline deepened (Figure 3-2). Both lakes had maximum rates of CO_2 evasion in late

October and evasion rates decreased slightly until cessation under ice cover. In lakes Croche and à l'Ours 67 and 57 % of the variability in carbon flux was explained by a negative relationship with temperature (Models 1 and 2, Table 3-2). In both lakes carbon flux was negatively correlated with respiration (r = -0.79, p<0.01, in Lac Croche and r = -0.46, p<0.10, in Lac à l'Ours).

Between mid-May and mid-November lakes Croche and à l'Ours emitted 3.86 x 10^6 g C and 5.03 x 10^6 g C to the atmosphere respectively. During ice break-up, we estimated the CO_2 flux from differences in concentrations between late March (just before break-up) and mid May (before stratification). About 2.69 x 10^6 g C (14 g C m^{-2}) from Lac Croche were lost to the atmosphere in the spring and 3.15 x 10^6 g CO_2 (21 g C m^{-2}) were emitted from Lac à l'Ours. Based on these estimates, Lac Croche and Lac à l'Ours contribute about 6.55 x 10^6 g C (34 g C m^2 y^{-1}) and 8.18 x 10^6 g C (55 g C m^2 y^{-1}) per year to the atmosphere, respectively.

Table 3-2. Linear regression models relating flux of carbon to the atmosphere (CO_2 flux, mg C m^2 d^{-1}), concentration (DIC, mg l^{-1}) or isotopic composition of dissolved CO_2 ($\delta^{13}C_{CO2}$, ‰) to temperature (T, °C), average photosynthetically available radiation on the day sampled (PAR, μE m^2 min^{-1}), depth of mixed layer (Z, m), pH, respiration (R, mg C m^2 d^{-1}), Chlorophyll-a (Chl-a, mg m^{-3}) and drainage ratio (DR). For models 1 and 2, n=23, for models 3-7, n= 103 and the ± symbol indicates standard error of the regression parameters.

Model	Dependant Variable	Regression	r^2	p
1	**CO_2 flux**[1]	-8.37±1.48 **T**+ 267.27±29.71	0.67	<0.001
2	**CO_2 flux**[2]	-14.13±2.89 **T**+ 445.34±59.12	0.57	<0.001
3	**CO_2 flux**	-73.90±21.51 log **PAR** + 7.21±2.59 **T** + 46.32±28.86 log **Z** + 379.12±155.19	0.23	<0.001
4	**DIC**	1.20±0.15 **pH** – 5.91±1.08	0.34	<0.001
5	**DIC**	0.34±0.08 log **R** +1.33 ± 0.38	0.09	<0.01
6	**$\delta^{13}C_{CO2}$**	4.08 ± 0.65 log **DIC** – 3.81±1.21 **pH** + 3.17±7.79	0.33	<0.001
7	**$\delta^{13}C_{CO2}$**	3.78 ± 0.65 log **DIC** – 4.76±1.15 **pH** + 1.27±0.41 log **Chl-a** –1.44±0.39 log **DR**+ 13.23±7.59	0.41	<0.001

[1]model for Lac Croche [2]model for Lac à l'Ours

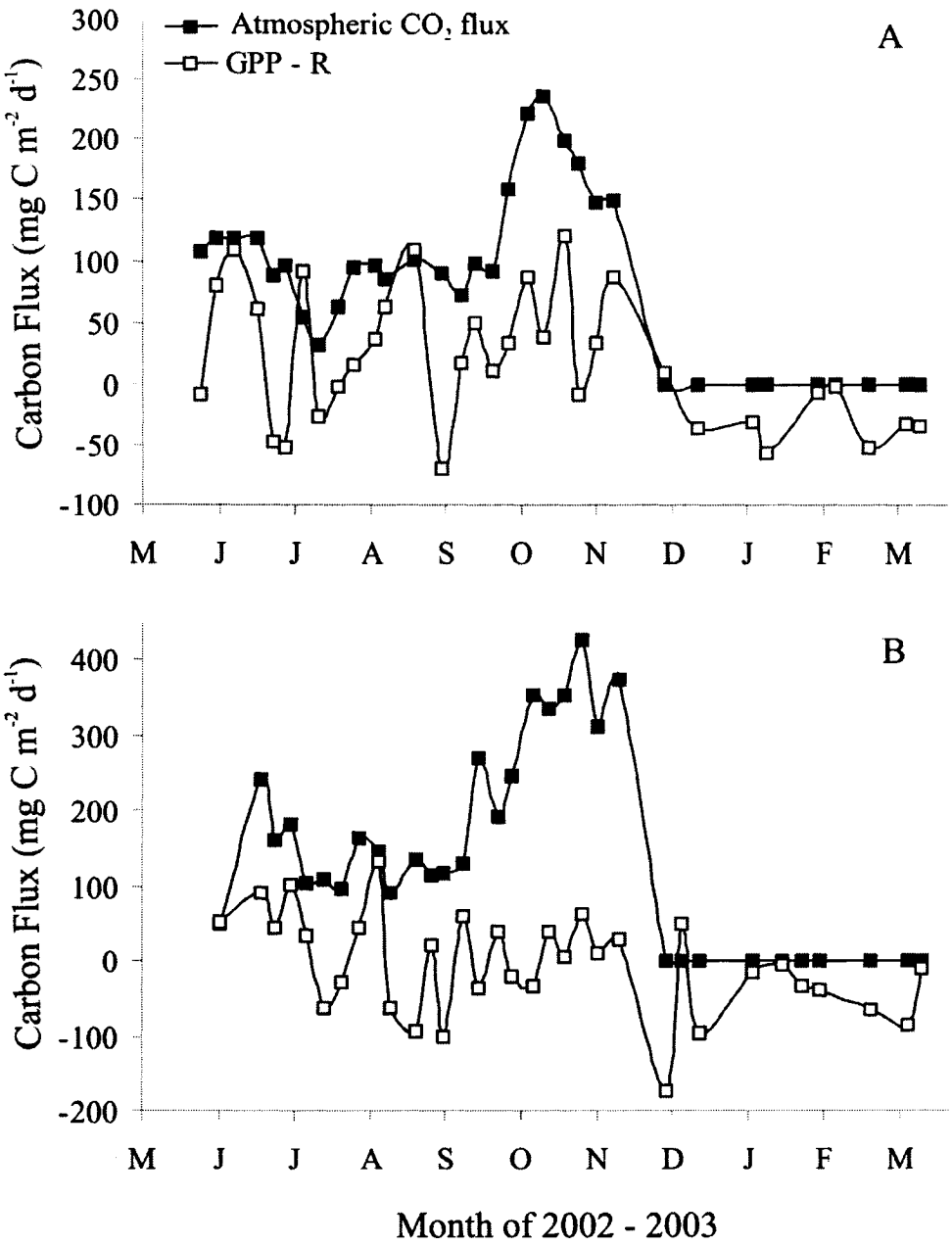

Figure 3-2. Flux of carbon dioxide to the atmosphere (mg C m^{-2} d^{-1}) and gross primary productivity minus respiration (GPP - R, mg C m^{-2} d^{-1}) from lakes Croche (A) and à l'Ours (B) between May 2002 and March 2003.

For the twenty-one lakes sampled in 2003, the degree of CO_2 saturation (CO_{2sat}) ranged from 0.54 to 7.96, averaging 2.52 (Figure 3-3, see Appendix 6 for additional data). Carbon flux ranged from –43 to 644 mg m^2 d^{-1}, averaging 148 mg m^2 d^{-1}. All of the lakes

were sources of CO_2 to the atmosphere over the ice-free season (Figure 3-4). Type I factorial analysis of variance was performed twice, once with the Laurentian lakes, where samples were taken monthly, and once with all lakes, where samples were taken in July, August and October. Analysis of variance of carbon flux of the Laurentian lakes, the lakes sampled on a monthly basis shows that carbon flux varied significantly over time ($p<0.001$, $df= 13$) but that there was more variation in carbon flux within lakes than between lakes ($p=0.56$, $df=5$). The sample analysis of variance performed on all the lakes sampled in May, July and October showed again that carbon flux varied significantly between months ($p<0.001$, $df=20$) but not significantly between lakes ($p=0.36$, $df=2$). CO_2 flux was lowest in May and June and highest in September and October (Figure 3-4). As we have no measures of early spring carbon dioxide concentrations, we did not attempt to estimate annual carbon flux from these lakes.

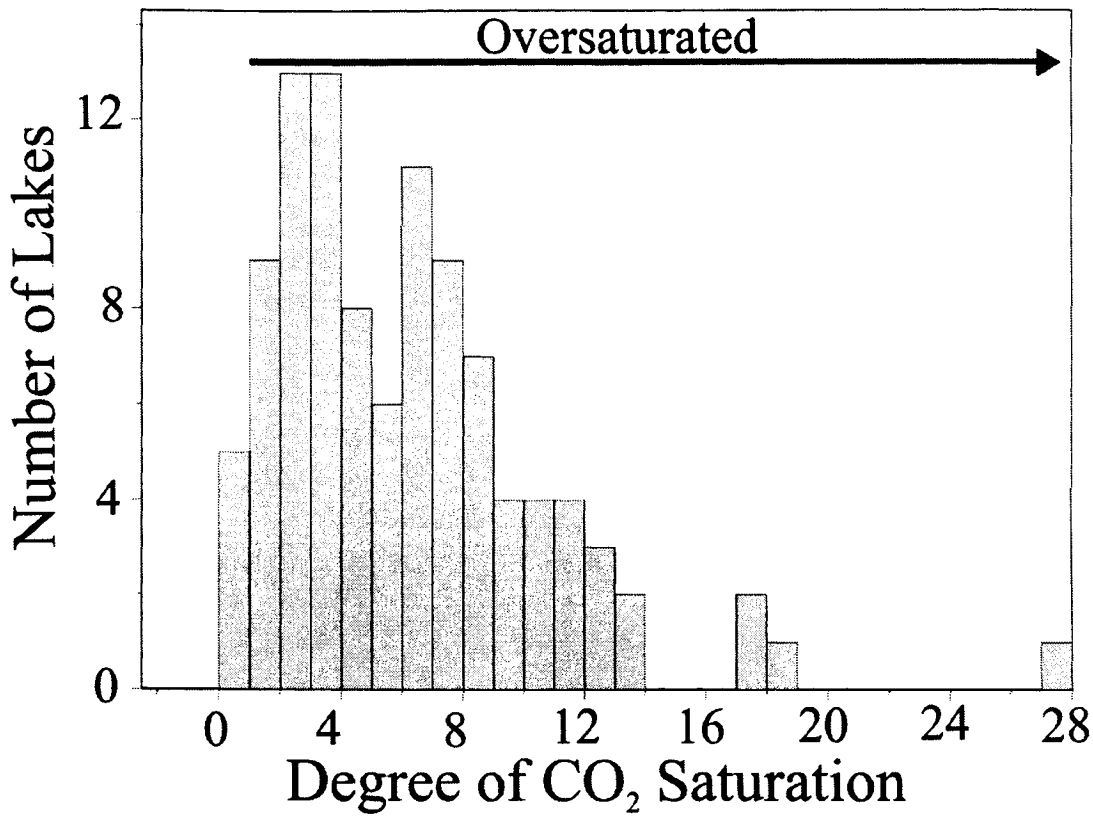

Figure 3-3. Carbon dioxide oversaturation (in number of times oversaturation) in the lakes sampled in 2003 (n=103).

Stepwise linear regressions were run with R, GPP, DOC, pH, temperature, PAR, chlorophyll-*a*, depth of mixed layer (e_z), mean depth and drainage ratio as effect variables. Carbon dioxide flux was dependent on depth of the mixed layer, temperature and PAR (Model 3, Table 3-2) though this model explains only 23 % of the variability in CO_2 flux. As pH is used to calculate carbon dioxide flux, it was not included in this stepwise linear regression. CO_2 flux was not significantly correlated with R (r=-0.12, p=0.12). Stepwise linear regression with total DIC as the dependent variable showed it was dependent on pH (Model 4, Table 3-2). There was a weak but significant positive relationship between total DIC and R (Model 5, Table 3-2).

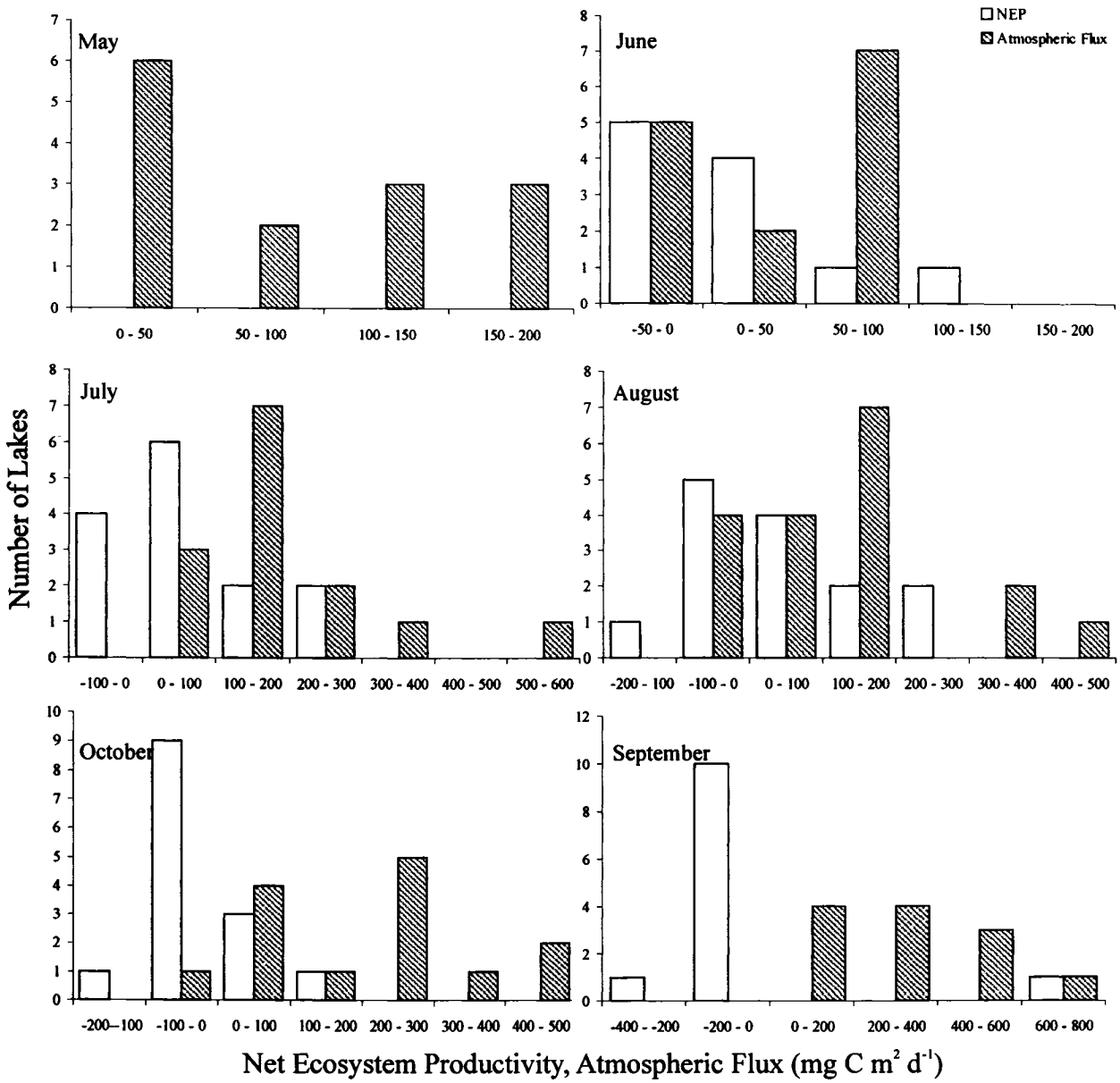

Figure 3-4. Difference between gross primary productivity and respiration (GPP - R, g C m^2 d^{-1}) and carbon flux to the atmosphere (mg C m^2 d^{-1}) in the twenty-one lakes sampled in 2003 (May n=21, June n=14, July n=21, August n=14, September n=14, October n=19).

GPP – R -

Whole lake GPP-R was calculated using measured epilimnetic production and respiration rates and, below the thermocline, changes in the concentration of oxygen over time (Appendix 7). For Lac Croche, R was greater than GPP in the spring, predominantly

less than GPP in summer and fall and greater than GPP throughout the winter (Figure 3-2). In Lac à l'Ours, GPP - R fluctuated widely in early summer, peaked in mid summer, fluctuated around equilibrium in the fall and R exceeded GPP throughout the winter. Over the ice-free season, the amount of carbon produced exceeded the amount of carbon consumed; whole-lake GPP - R was 1.2 x 10^6 g C (37±23 mg C m^{-2} d^{-1}) in Lac Croche and 0.4 x 10^6 g C (14±26 mg C m^{-2} d^{-1}) in Lac à l'Ours. In Lac Croche GPP - R between December and March was –0.6 x 10^6 g C (-25±17 mg C m^{-2} d^{-1}). In Lac à l'Ours GPP - R was –0.6 x 10^6 g C (-33±30 mg C m^{-2} d^{-1}) in the winter; winter respiration exceeded summer net primary productivity.

The difference between GPP and R for the 14 Laurentian lakes sampled on a monthly basis in 2003 ranged from –282 to 873 mg C m^{-2} d^{-1} and averaged 11±36 mg C m^{-2} d^{-1} (Table 3-3, Appendix 6). The excess of GPP over R was highest in midsummer and R was greater than GPP in October (Figure 3-4). Type I factorial analysis of variance shows there is significant variation between lakes (df=13, p=0.03) and between months (df=4, p<0.001). Application of the winter estimates of GPP - R from lakes Croche and à l'Ours to the lakes sampled in 2003 as an approximation shows that on an annual basis R exceeds GPP in most of the lakes sampled. However, for all lakes, the magnitude of carbon dioxide produced in the water column over an entire year by respiration is not sufficient to account for the magnitude of the CO_2 flux to the atmosphere during the ice-free season (Table 3-3). Furthermore, there is no significant correlation between the atmospheric flux of CO_2 and GPP - R during the ice-free season for the Laurentian lakes sampled in 2003 (n=70, r=-0.12, p=0.19).

Table 3-3. Carbon fluxes of the lakes sampled. Lake area (LA, km^2), number of samples (*n*), length of sampling period (sampling period, d), average flux of carbon dioxide to the atmosphere ($A_{average}$, mg C m^2 d^{-1}), total flux of CO_2 to the atmosphere over the sampling period (A_{total}, t C), average GPP - R over the sampling period (GPP - $R_{average}$, mg C m^2 d^{-1}), total GPP - R over the sampling period (GPP - $R_{ice\text{-}free}$, t C) and estimated GPP - R over the year (GPP - R_{annual}, t C y^{-1}). Confidence intervals are at the α=0.05 critical level.

Lake	Lake Area	*n*	Sampling Period	$A_{average}$	A_{total}	GPP - $R_{average}$	GPP - $R_{ice\text{-}free}$	GPP - R_{annual}
Croche	0.19	26	174	124±25	4.1	37±23	1.2	1.0
Ours	0.15	25	174	207±55	5.4	14±26	0.4	-0.2
Achigan	5.31	6	160	145±127	123.3	-108±102	-113.0	-120
Blanche	0.41	6	165	136±110	9.2	-59±101	-4.8	-8.9
Connelly	1.24	5	114	146±130	20.7	-54±78	-13.0	-19.4
En Coeur	0.87	5	118	53±67	2.8	33±125	3.0	1.8
Gervais	0.45	6	166	187±153	29.9	100±553	19.0	-5.8
Mont. Noire	0.97	6	162	199±159	92.1	-16±16	-8.8	-13.1
du Nord	2.80	6	162	187±213	26.2	19±95	3.3	-1.8
Ouimet	1.56	6	169	258±296	67.9	-40±76	-12	-16.2
Pin Rouge	0.15	6	151	86±79	2.0	48±174	1.5	0.8
Rouge	0.68	6	165	145±161	16.1	-19±214	-2.5	-7.7
des Sables	2.96	6	165	239±187	116.7	-14±83	-8.1	-17.1
St. Joseph	1.47	6	157	152±114	35.0	-0.7±38	-0.2	-4.7
Tremblant	9.56	6	169	162±156	261.8	-28±61	-53	-132.2
Truite	0.51	6	165	230±159	19.4	35±223	3.6	-1.2
d'Argent	1.00	3	171	332±323	85.1			
Bowker	2.30	3	171	67±28	11.4			
Brome	14.50	3	172	120±199	47.7			
Orford	1.30	3	171	260±64	645.8			
Waterloo	1.50	3	172	102±217	22.8			
La Pêche	7.05	3	150	220±158	56.8			
Phillippe	1.72	3	150	108±249	113.7			

Carbon Isotopes -

During the ice-free season, $\delta^{13}C_{CO2}$ in Lac Croche ranged between –9.4 and –21.3 ‰ and averaged –14.5 ± 0.76 ‰. In Lac à l'Ours $\delta^{13}C_{CO2}$ ranged between –7.1 and –17.3 ‰ during the ice-free season and averaged –12.1 ± 0.4 ‰. In both lakes $\delta^{13}C_{CO2}$ in the ice-free period was enriched over $\delta^{13}C_{CO2}$ under icecover, which averaged –20.6 ± 0.9 ‰ in Lac Croche and –17.5 ± 1.1 ‰ in Lac à l'Ours. If respiration is the major source of the inorganic carbon in lakes, then the isotopic composition of CO_2 should reflect this input. Because respiration consumes already isotopically depleted organic carbon without fractionation, it causes the DIC pool to become increasingly depleted in ^{13}C. Thus, in a system where respiration is the major source of DIC, a negative correlation between the concentration of DIC and $\delta^{13}C_{CO2}$, should exist (Figure 3-1). However, over the ice-free season Lac Croche showed a positive correlation between $\delta^{13}C_{CO2}$ and DIC (r=0.55, p<0.01) and Lac à l'Ours showed no correlation between these variables (r=-0.17, p=0.39). There also was no significant correlation between R and $\delta^{13}C_{CO2}$ in lakes Croche or à l'Ours (r=0.03, p=0.47 and r=-0.08, p=0.35) during the ice-free season. In contrast, under ice-cover, both lakes Croche and à l'Ours did show a negative correlation between $\delta^{13}C_{CO2}$ and the concentration of DIC (r=-0.76, p<0.01 and r=-0.452, p<0.10). Respiration appears to dominate carbon dynamics in the lakes during the winter.

For the 21 lakes sampled in 2003, the isotopic value of $\delta^{13}C_{CO2}$ ranged from –25.2 to –4.9‰, with an average of –13.3‰. The lakes in the Laurentians, Gatineau and Eastern Townships show regional differences in $\delta^{13}C_{CO2}$ values. A single classification ANOVA shows theses variations are statistically significant (p<0.001). Dissolved CO_2 in the

Laurentian lakes, where there are very few carbonates in the lakes' watersheds, was on average more isotopically depleted than in the other regions.

The relationship between $\delta^{13}C_{CO2}$ and CO_{2sat} for the 21 lakes sampled in 2003 is presented in Figure 3-5A. Again, the degree of CO_2 saturation and the isotopic value of the CO_2 are not negatively but positively correlated on a semi-log scale (r=0.49, p<0.001). To eliminate the possibility that dissolution of carbonates was causing this correlation, the same test was run solely for the Laurentian lakes, which have no carbonate bedrock, and their $\delta^{13}C_{CO2}$ and CO_{2sat} were positively correlated as well (r=0.50, p<0.001).

Stepwise linear regression showed that total DIC and pH explained 33% of the variability in $\delta^{13}C_{CO2}$ (Model 6, Table 3-2) and the inclusion of the lake drainage ratio (watershed area/lake area), and chlorophyll *a* explained an additional 8% of the variability (Model 7, Table 3-2).

Like lakes Croche and à l'Ours, $\delta^{13}C_{CO2}$ and R in the lakes sampled in 2003 did not exhibit the negative trend that would be expected if respiration were the dominant cause of carbon dioxide oversaturation (Figure 3-5B); there was no significant correlation between the variables (r=0.04, p=0.67). There are two obvious outliers amongst the respiration data (Figure 3-5B), both from unstratified Eastern Township lakes. When these data points are removed from the set there is still no significant correlation between R and $\delta^{13}C_{CO2}$ (r=0.054, p=0.60).

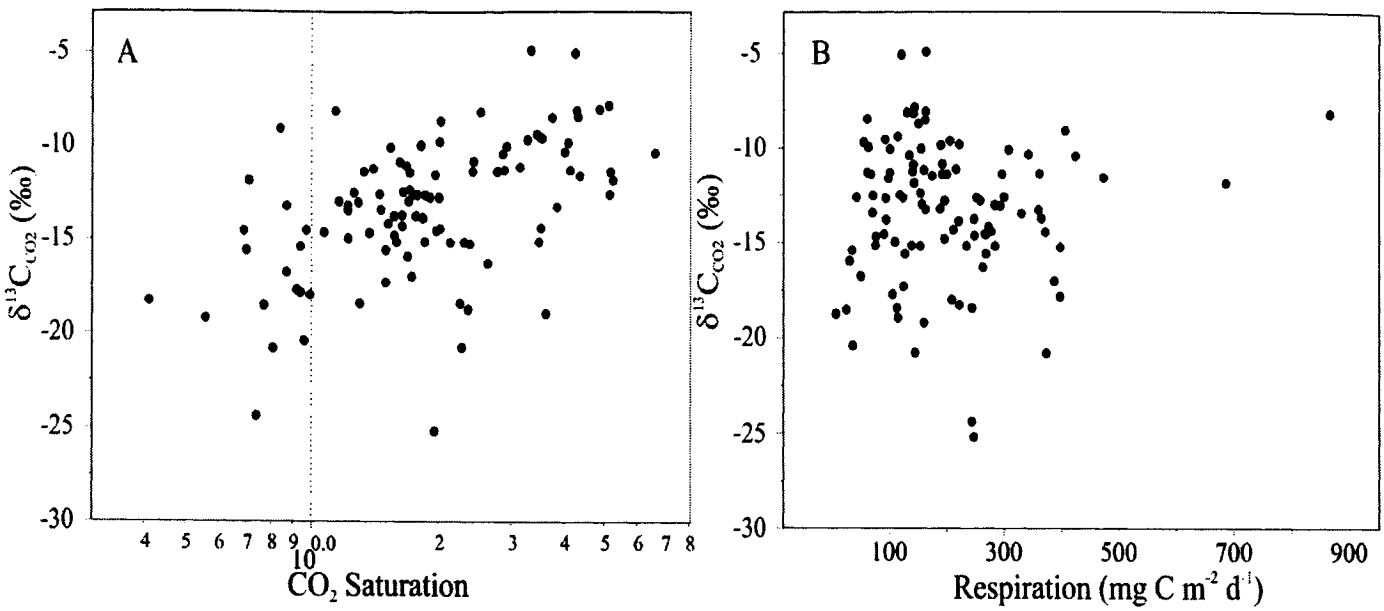

Figure 3-5. Isotopic composition of dissolved CO_2, $\delta^{13}C_{CO2}$, versus CO_2 saturation (A, dotted line indicates CO_2 equilibrium) and community respiration (B, mg C m^{-2} d^{-1}) measured in the mixed layer.

Carbon Mass Balance -

We applied the model proposed by Bade et al. (2004) to our data from lakes Croche and à l'Ours to give $\delta^{13}C_{DIC}$ that results from measured rates of respiration, production and atmospheric exchange. If we consider the difference between the $\delta^{13}C_{DIC}$ predicted by the model and the observed $\delta^{13}C_{DIC}$ to be the result of external inputs of DIC, we can determine if the source of excess DIC is enriched or depleted relative to $\delta^{13}C_{DIC}$ of lake water. In Lac Croche, predicted values of $\delta^{13}C_{DIC}$ were more enriched than observed values in seventy-five percent of cases, with averages of 7.6 ± 24.7 and –13.0 ± 1.6 ‰, respectively (Table 3-4). The difference between observed and predicted $\delta^{13}C_{DIC}$ indicates a ^{13}C-depleted source of excess DIC in Lac Croche. Conversely, in Lac à l'Ours, the predicted values of $\delta^{13}C_{DIC}$ were more isotopically depleted than the observed values in 56% of cases; average predicted

$\delta^{13}C_{DIC}$ was -13.2 ± 21.0 ‰ while average observed $\delta^{13}C_{DIC}$ was –7.9 ± 0.7 ‰. The difference between observed and predicted $\delta^{13}C_{DIC}$ indicates a ^{13}C-enriched source of excess DIC in Lac à l'Ours.

Table 3-4. Carbon parameters from Bade et al.'s (2004) process based model. $\delta^{13}C_{obs}$ = observed isotopic composition of DIC, $\delta^{13}C_{pred}$ = predicted isotopic composition of DIC, $\delta^{13}C_{GW}$ = isotopic composition of DIC measured in groundwater, $[DIC]_{GW}$ = measured concentration of DIC in groundwater (mg L^{-1}), GW input = estimated groundwater input from difference between observed and predicted $\delta^{13}C_{DIC}$ (cm m^{-2} d^{-1}).

Lake	$\delta^{13}C_{obs}$	$\delta^{13}C_{pred}$	$\delta^{13}C_{GW}$	$[DIC]_{GW}$	GW input
Achigan*	-5.4	4.8	-16.5	5.6	1.5
Blanche*	-12.1	13.7	-12.4	11.6	2.4
Connelly*	-8.3	36.1	-14.7	44.6	5.1
En Coeur*	-7.3	-25.7	-14.0	16.6	
Gervais*	-4.6	-16.1			
Montagne Noire*	-6.3	-21.4	-10.8	14.3	
du Nord*	-8.7	-21.6	-14.5	23.4	
Ouimet*	-5.1	20.2	-14.9	21.8	0.2
Pin Rouge*	-8.1	32.8	-10.3	27.7	0.7
Rouge	-8.7	49.4			1.9
des Sables	-7.3	1.6			0.1
St. Joseph*	-11.6	42.3	-15.3	19.7	0.5
Tremblent	-12.0	-22.7			
Truite	-5.0	3.4			0.3
D'argent*	-5.4	-17.9	-10.4	28.1	
Bowker*	-4.1	-34.3	-9.0	10.0	
Brome*	-2.6	-25.0	-8.8	35.0	
Orford*	-0.3	-28.9	-2.7	5.3	
Waterloo*	-2.8	-0.6	-11.1	66.7	0.01
la Pêche*	-1.9	3.8	-7.4	21.0	0.1
Phillippe	-1.6	-33.0			
Croche*	-13.0	-7.6	-19.1	4.1	0.4
Ours*	-7.9	-13.2	-11.0	21.3	

*Indicates lakes where groundwater samples were taken from the watershed.

Applying the model to the lakes sampled in 2003 shows there is wide variation in the difference between the theoretical and the observed value of $\delta^{13}C_{DIC}$. For eleven of the twenty-one lakes, Bade's model predicts an average $\delta^{13}C_{DIC}$ that is more enriched than the observed value, indicating a lighter source of DIC as the cause of carbon dioxide oversaturation. For the other ten lakes Bade et al.'s (2004) model predicts values that are on average 19‰ more negative than observed values of $\delta^{13}C_{DIC}$. If the differences between predicted and observed values are truly due to external inputs, the external inputs must have a more enriched $\delta^{13}C_{DIC}$ composition.

Groundwater often becomes supersaturated in CO_2 as it percolates through carbon rich soils and thus is a plausible source of CO_2 to lakes. We sampled groundwater in the basins of sixteen lakes for CO_2 saturation and carbon isotopes (Table 3-4). Groundwater $\delta^{13}C_{DIC}$ was consistently more isotopically depleted than lake water $\delta^{13}C_{DIC}$ and concentrations of DIC were higher than lake waters, averaging 22.7 ± 3.3 mg L^{-1}. If we consider the disparity between the model's predicted values and observed values of $\delta^{13}C_{DIC}$ to be the consequence of groundwater inputs of DIC, then we can estimate the input into the lake from its $\delta^{13}C_{DIC}$. In Lac Croche, $\delta^{13}C_{DIC}$ of groundwater was measured from twelve wells in the lake watershed, with an average $\delta^{13}C_{DIC}$ value of -19.2 ± 3.1 ‰ and an average concentration of DIC of 4.1 ± 2.7 mg L^{-1}. With these values, the average input of groundwater into Lac Croche would be 735 m^3 d^{-1}, or 0.4 cm over the surface area of the lake per day. For the eleven lakes sampled in 2003 where a depleted source of DIC is predicted, the amount of groundwater input necessary to account for the disparity between observed and predicted $\delta^{13}C_{DIC}$ ranges from 1 mm (in Lake Waterloo) to 5.1 cm (in Lac Connelly) over the lake surface area per day. For the other ten lakes sampled in 2003, Bade

et al.'s (2004) model predicts an enriched source of DIC. While we do not have groundwater samples from all watersheds, groundwater $\delta^{13}C_{DIC}$ was consistently more isotopically depleted than lake waters and thus, according to this model, is not the likely source of carbon dioxide oversaturation in the lakes.

Discussion

Carbon dioxide concentrations -

Estimates of carbon dioxide saturation for the lakes sampled during the ice-free season of 2003 were similar to previously reported values. Carignan (1998b) found Lac Croche to be typically oversaturated with CO_2. del Giorgio and Peters (1994) found lakes Bowker, Brome, d'Argent, and Orford to be oversaturated with CO_2 during the summer. However, they found that Lake Waterloo was on average undersaturated while we found it to be on average oversaturated in CO_2. Wang and Veizer (2000, 2004) report values of CO_2 concentrations up to 20 times greater than atmospheric values in Meech Lake, in the Gatineau region of Quebec, near lakes Phillippe and LaPeche. While we did not find values this high in lakes Phillippe and LaPeche, we also found the Gatineau lakes were oversaturated in CO_2.

Carbon flux -

Our estimates of carbon flux from lakes Croche and a l'Ours, 34 g C m^{-2} y^{-1} and 55 g C m^{-2} y^{-1}, are generally in agreement with other studies. Cole et al. (1994) estimated carbon evasion from lakes globally to be 70 g C m^{-2} y^{-1}. Amazon basin rivers and wetlands outgas about 120 g C m^{-2} y^{-1} (Richey et al. 2002). A survey of arctic lakes (Kling et al. 1991) found average carbon evasion to be 90 g C m^{-2} y^{-1}. Despite our simple methodology for estimating carbon dioxide flux after spring ice melt, our results were similar to other reported values.

We estimated springtime flux from Lac Croche to be 14 g C m^{-2} and 21 g C m^{-2} from Lac à l'Ours. Striegl et al. (2001) found flux after ice break-up to be 30 g C m^{-2} on average from lakes in Finland and 29 g C m^{-2} for a set of lakes in the United States.

The gas transfer velocity, k, used in this study to estimate CO_2 flux was measured by Cole and Caraco (1998) in a small oligotrophic lake. They found that gas exchange was independent of wind speed at low wind speeds and average was k_{600} 0.636 ± 0.029 m d^{-1}. During the ice-free season, wind speed at Lac Croche averaged 1.79 ± 0.05 m s^{-1}, showing this estimates of k is applicable for the small lakes in our study. Crusius and Wanninkhof (2003) also examined gas transfer velocity in a small oligotrophic lake and concluded that a bilinear model with a break point at 3.7 m s^{-1} best fits the relationship between wind speed and k. Using k from this relationship in our calculations lowers our estimates of carbon flux during the ice-free season by 0.6% in Lac Croche and raises it by 3% in Lac à l'Ours. The difference in k has a larger effect on spring estimates of carbon flux and raises our annual estimates of carbon flux by 6 and 12 % in lakes Croche and à l'Ours.

While the constant gas transfer velocity from Cole and Caraco (1998) is applicable for the smaller lakes studied in 2003, it may be less reasonable for larger lakes where wind speeds may be higher. As wind speed increases, k increases (Crusius and Wanninkhof 2003) and carbon dioxide fluxes would be higher. However, it is unlikely that wind speeds even on these larger lakes are frequently greater than 3.7 m s^{-1}. Environment Canada measures wind speeds from anemomenters installed at 10 m height in open areas. They report average wind speed between May and October of 1970 to 1992 was 2.60 m s^{-1} at Ste. Agathe des Monts, a town in the centre of the Laurentian study area. Average wind speed between May and October for Sherbrooke, in the Eastern Townships, was 2.28 m s^{-1} between 1971 and 2000.

None of the variables included in our stepwise linear regression explained a large amount of the variability in carbon flux or total DIC of the lakes sampled in 2003. Though temperature and carbon flux were negatively correlated in lakes Croche and à l'Ours, temperature only explained a minor amount of variability in carbon flux in the lakes sampled in 2003. The relationship between the concentration of dissolved inorganic carbon and respiration was significant but weak, suggesting that respiration is not the main source of inorganic carbon in the lakes.

GPP – R -

Comparing annual estimates of GPP - R to estimates of atmospheric flux of carbon shows that an excess of R over GPP is not sufficient to account for the flux of carbon to the atmosphere. In Lac Croche GPP was greater than R by 1.0×10^6 g C y^{-1} while the flux of CO_2 to the atmosphere was 6.6×10^6 g C y^{-1}, so that in Lac Croche external sources must provide an excess 7.6×10^6 g C y^{-1} (40 g C m^{-2} y^{-1}). In Lac à l'Ours R exceeded GPP by -0.5×10^6 g C y^{-1}, but the excess was not in the same order of magnitude as the flux of carbon to the atmosphere, 8.2×10^6 g C y^{-1}. In Lac à l'Ours external sources of DIC must provide a total of 7.7×10^6 g C y^{-1} (51 g C m^{-2} y^{-1}) to account for the flux of C to the atmosphere and the C used in GPP.

Our estimates of GPP - R are not entirely consistent between the mixed layer and the hypolimnion. While estimates for GPP - R in the hypolimnion include all processes that consume O_2 (water column respiration as well as chemical oxidation and benthic respiration), estimates of GPP - R in the mixed layer do not include photooxidation nor respiration or production of macrophytes or benthic organisms in the littoral zone. As a sensitivity analysis we doubled the rates of respiration in the epilimnion, without increasing production rates, and re-calculated GPP - R. While R was greater than GPP for all lakes over

the sampling period, this excess of respiration over production was still not sufficient to account for the carbon flux to the atmosphere. For example, with respiration rates doubled in Lac Croche, annual GPP - R changed from 953 kg C to –3250 kg C, but this could not account for the annual loss of to the atmosphere of 6445 kg C. In Lac à l'Ours, doubling epilimnetic R changes annual GPP - R from –553 kg C to –5726 kg C, which is again insufficient to account for the annual flux to the atmosphere of 8181 kg C.

A photosynthetic quotient (PQ) of 1.25 (mole O_2 per mole C produced or respired) was used to express GPP - R, derived from oxygen production and consumption rates, as carbon equivalents. However, literature values for photosynthetic quotients vary widely (e.g. Williams and Robertson 1991). Using a PQ of 1 (del Giorgio and Peters 1994), GPP - R is on average greater by 30 mg C m^{-2} d^{-1} while a PQ of 1.6 (Bell and Kuparinen 1984) decreases GPP - R by 6 mg C m^{-2} d^{-1}. Even with a larger PQ, respiration did not exceed production by a sufficient amount to account for the atmospheric flux of carbon.

Carbon Isotopes -

Further evidence that net heterotrophy is not the major cause of carbon dioxide oversaturation comes from the isotopic composition of the dissolved CO_2, which does not show the signal of excess respiration. While respiration produces a lighter CO_2 pool, production preferentially consumes the light isotope of carbon leaving the CO_2 pool heavier (Figure 3-1). In the 2003 lakes we found a positive correlation between $\delta^{13}C_{CO2}$ and CO_{2sat}. A recent study of 32 lakes in the Wisconsin and Michigan (Bade et al. 2004) also shows this trend. When their $\delta^{13}C_{DIC}$ data are corrected for pH, there is a significant correlation between $\delta^{13}C_{CO2}$ and DIC (r^2=0.79, df= 39, p<0.05). As the amount of inorganic carbon in the system increases, the isotopic composition of this carbon is more enriched: the

opposite of what would occur if respiration were the cause. This indicates that ^{13}C depletion caused by respiration is balanced out by the photosynthetic enrichment in ^{13}C, requiring a third process for input of carbon dioxide into the system. Striegl et al. (2001) also analyzed pCO_2 and $\delta^{13}C_{DIC}$ from 132 northern lakes and found lakes with the greatest pCO_2 had the lightest $\delta^{13}C_{DIC}$, which they concluded was an indication of respiration as a primary source of CO_2. However, because they did not account for the effect of pH on carbonate speciation and thus on the isotopic composition of DIC, this cannot be assumed. Holding the concentration of DIC and the isotopic composition of dissolved CO_2 constant, lakes with high pH would necessarily have lower pCO_2 and more depleted $\delta^{13}C_{DIC}$.

Carbon Mass Balance -

We used the process-based model for $\delta^{13}C_{DIC}$ proposed by Bade et al. (2004) to elucidate the source of excess carbon dioxide. For all the lakes, the predicted and observed values of $\delta^{13}C_{DIC}$ did not match, indicating that production, respiration and atmospheric exchange are not the only controls of DIC in the lakes. Concentrations of DIC in groundwater were on average ten times greater than in the mixed layer of lakes. For eleven of the twenty-three lakes sampled predicted values of $\delta^{13}C_{DIC}$ were more enriched than observed values of $\delta^{13}C_{DIC}$, indicating a depleted source of excess inorganic carbon. If we consider groundwater to be an input of DIC, our estimates of groundwater input into lakes these lakes averaged 1.1 ± 0.86 cm d^{-1}, are similar to reported values for other northern temperate lakes. Cole and Pace (1998) found that groundwater input into three Michigan lakes averaged 0.48 ± 0.36 cm d^{-1}. In over half of the lakes sampled, our measures of the isotopic composition of DIC in groundwater show that it is a possible source of the CO_2.

For the other lakes sampled in 2003, Bade et al.'s model predicts values that are on average 19‰ more negative than the observed values of $\delta^{13}C_{DIC}$. Thus, if the difference between predicted and observed values is truly due to external inputs, these external inputs must have a more enriched $\delta^{13}C_{DIC}$ composition. While we do not have groundwater samples from all watersheds, groundwater $\delta^{13}C_{DIC}$ were consistently more isotopically depleted than lake waters and thus is not the likely source. Also, not all the external inputs of DIC are attributable to groundwater; overland flow and stream inputs were not included in our model and may be enriched inputs of DIC. For example, methane production in an upstream wetland or the littoral zone will enrich the dissolved CO_2 pool, which may then be transported into the lake system.

A third possibility to explain the disparity between the observed and the theoretical $\delta^{13}C_{DIC}$, is that the parameters of Bade et al.'s model do not adequately describe carbon dynamics in these lakes. The model frequently predicts $\delta^{13}C_{DIC}$ outside of the range normally observed in freshwater and assumes 90% of GPP is respired, though it is very sensitive to this percentage.

Conclusions

Of the twenty-three Québec lakes sampled, we found most were oversaturated in carbon dioxide and thus net sources of CO_2 to the atmosphere. From carbon flux data of lakes Croche and à l'Ours, two lakes sampled on a weekly basis for a year, we found these lakes emit about 45 g C m^2 y^{-1}. On an individual basis this emission seems negligible but when one considers that 891163 km^2 of Canada alone is covered by freshwater, the total flux can be estimated at 4×10^{13} g C y^{-1}. Ciasis et al. (1995) estimated the missing carbon sink postulated for the northern hemisphere to be about 3.5×10^{15} g C y^{-1}. More recently, Liski et

al. (2003) proposed that 0.88×10^{15} g C y^{-1} are sequestered by temperate and boreal forests, for a net carbon sink by forests in Canada of about 1.0×10^{14} g C y^{-1}. Since our, albeit rough, estimate of carbon emissions from freshwater ecosystems is within a factor of 2.5 of this number, a compensating carbon flux from terrestrial aquatic systems should no longer be ignored.

Despite the general trend of lake oversaturation, we found little evidence to conclude that this carbon dioxide oversaturation was the exclusive result of net heterotrophy, of in situ respiration exceeding production. First, while respiration rates were often as large as carbon flux in lakes Croche and à l'Ours, the respiration and carbon fluxes were negatively correlated. This implies that a large portion of the CO_2 generated in situ must have been consumed by production rather than have evaded to the atmosphere. It also suggests that a second process is controlling carbon flux and respiration in an opposite manner. We found that increasing temperature resulted in significantly higher respiration rates and significant decreases in the carbon flux. In the lakes sampled in 2003, carbon flux was not a function of respiratory flux. Secondly, the isotopic composition of dissolved CO_2 did not present evidence of respiration dominance. $\delta^{13}C_{CO2}$ and carbon flux were positively correlated and there was no significant relationship between R and $\delta^{13}C_{CO2}$. Our calculations of whole-lake GPP – R show that in situ respiration does not supply adequate CO_2 to account for the atmospheric flux and external inputs of DIC must be subsidizing the lake to explain the continued CO_2 oversaturation. According to the process-based model of Bade et al. (2004), respiration, production and atmospheric exchange alone are not sufficient to explain the isotopic composition of inorganic carbon in the lakes; external inputs also influence $\delta^{13}C_{DIC}$.

The inadequacy of in situ respiration as an explanation for carbon dioxide oversaturation is not unique to the Quebec lakes studied. A study of four closed-basin lakes in northern Wisconsin lakes (Riera et al. 1999) found that in lake respiration was insufficient to explain the evasion of carbon dioxide to the atmosphere. Jonsson et al. (2003) also found that pelagic respiration in 51 Swedish lakes was not sufficient to account for the carbon flux to the atmosphere.

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General Conclusions

Stables isotopes of dissolved oxygen can be used to determine the metabolic balance of aquatic systems (Quay et al. 1995; Luz et al. 2000). However, this methodology has not been rigorously compared to traditional methods of metabolic measurements. We proposed two stable isotope methods to examine metabolism in aquatic systems. The $\delta^{18}O$ method uses stable isotopes of oxygen, the degree of oxygen saturation and bottle incubation measurements of respiration to measure gross primary production. Comparing results from this model with traditional bottle incubation methods shows the $\delta^{18}O$ method provides analogous results with several advantages; the method required less laboratory time, smaller sample volumes and is more easily applied to remote areas. However, because bottle incubations are used to measure respiration, this model does not completely take into account benthic or littoral processes and thus is most applicable as a measure of planktonic metabolic processes. Also, while the $\delta^{18}O$ method is appropriate for these oligotrophic lakes where the assumption that the aquatic system is sufficiently large to smooth short duration variations of $^{18}O_{DO}$, $^{18}O_W$, R, K_{O2}, O_2 and α_s, a dynamic model may be required in systems with rapid fluctuations.

The $\delta^{13}C$ method uses stable isotopes of both carbon and oxygen and the degree of carbon and oxygen saturation to estimate both gross primary production and respiration. This method is not constrained by bottle incubations to measure respiration and thus takes into account benthic and littoral metabolic processes and integrates samples over the residence time of oxygen and carbon dioxide in the system, leading to a whole-lake estimate of metabolism. Because of this, measures of metabolism from this model are not strictly comparable with measures of metabolism from traditional methods such as the Winkler

method or ^{14}C incubations. The $\delta^{13}C$ method is limited by the assumed isotopic signature of respired carbon, which may have a significant effect on estimates of GPP and R. However, the most severe limitation of the $\delta^{13}C$ method is that the model does not adequately describe carbon dynamics in the lakes; external inputs of inorganic carbon are not accounted for. As shown, minor inputs of external carbon to the aquatic system will have a large effect on estimates of GPP and R from the $\delta^{13}C$ method. In systems with significant allochthonous carbon inputs, the $\delta^{13}C$ method cannot be accurate unless these inputs are accounted for.

Using the $\delta^{18}O$ method, we measured metabolism in twenty-one lakes in three regions of Québec. Multiple lines of evidence demonstrate that net heterotrophy is not a general occurrence in northern temperate lakes. Firstly, the epilimnia of the study lakes were frequently oversaturated in oxygen during the summer months and the isotopic composition of the dissolved oxygen provides evidence that production dominance was a likely source of the oxygen oversaturation. Secondly, the slope of the relationship between planktonic R and GPP was significantly less than 1 and its intercept was not significantly different from 0, indicating that pelagic GPP fuels planktonic R. More than half of the lakes sampled developed metalimnetic oxygen peaks during the summer months: a phenomenon that could only occur if GPP was greater than R even below the thermocline. Finally, the $\delta^{18}O$ method showed GPP dominated over R during the ice-free season, average GPP:R was 1.12±0.13.

GPP, R, and the balance between GPP and R were all most strongly correlated with lake temperature, which in turn is a function of the amount of solar radiation received by the lake. Our results imply that it is this solar radiation that drives pelagic gross primary productivity, which in turn drives the majority of pelagic respiration. Recent studies have stressed the importance of DOC as substrate for heterotrophic bacteria. However we found

variation in DOC only explained 8% of the variation in pelagic R, while variation in pelagic GPP explained approximately 80% of the variation in pelagic R, indicating that primary production is at the base of the food web rather than allochthonous inputs of carbon. We did not find evidence that moderate levels of DOC, between 6 and 10 mg L^{-1} lead to net heterotrophy. Though our number of samples is limited, we did find net heterotrophy in lakes with DOC levels above 10 mg L^{-1}.

Despite this general trend of net autotrophy we found lakes were commonly oversaturated in carbon dioxide. A study of carbon dynamics in 23 Quebec lakes was carried out to determine the magnitude of carbon flux to the atmosphere from these lakes and to examine the underlying cause for carbon dioxide oversaturation. The magnitude of atmospheric flux, gross primary production and community respiration were measured, as well as the isotopic composition of dissolved carbon. All of the lakes sampled were, on average, oversaturated with carbon dioxide over the sampling period. However, we found little evidence to conclude this carbon dioxide oversaturation was the result of an excess of in situ respiration over production. First, the magnitude of the annual excess of R over GPP was not sufficient to account for the flux to the atmosphere. Carbon evasion was not a function of respiratory flux, nor did the isotopic signature of dissolved CO_2 in the lakes present evidence of respiration. Groundwater inputs of carbon dioxide represent a plausible source for carbon dioxide oversaturation in some, but not all, of the lakes sampled.

Of the twenty-three Québec lakes sampled, we found most to be oversaturated with respect to carbon dioxide and thus net sources of CO_2 to the atmosphere. From carbon flux data of lakes Croche and à l'Ours, two lakes sampled on a weekly basis for a year, we found these lakes emit about 45 g C m^2 y^{-1}. On an individual basis this emission seems negligible but when one considers that 891 163 km^2 of Canada alone is covered by freshwater, the total

flux can be estimated at 4 x 10^{13} g C y^{-1}. Ciasis et al. (1995) estimated the missing carbon sink postulated for the northern hemisphere to be about 3.5 x 10^{15} g C y^{-1}. More recently, Liski et al. (2003) proposed that 0.88 x 10^{15} g C y^{-1} are sequestered by temperate and boreal forests, for a net carbon sink by forests in Canada of about 1.0 x 10^{14} g C y^{-1}. Since our, albeit rough, estimate of carbon emissions from freshwater ecosystems is within a factor of 2.5 of this number, a compensating carbon flux from terrestrial aquatic systems should no longer be ignored.

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Appendix 1 Derivations of equations and error calculations

Derivation of Equation 4

The change in oxygen concentration over time is expressed as:

$$\frac{d[O_2]}{dt} = GPP - R - \frac{K_{O_2}}{Z}(O_2 - O_{2sat}) \quad 2.$$

Note that equation numbers correspond with equation numbers in Chapter 1. Each component of equation 2 is multiplied by its respective isotopic ratio to give the isotope mass balance:

$$\frac{d[O_2]^{18}O_{DO}}{dt} = GPP^{18}O_P - R^{18}O_R - \frac{K_{O_2}}{Z}\alpha_G(O_2{}^{18}O_{DO} - O_{2sat}{}^{18}O_A\alpha_s) \quad 3.$$

Expanding equation 3 gives:

$$\frac{d[O_2]}{dt}{}^{18}O_{DO} + \frac{d^{18}O_{DO}}{dt}[O_2] = GPP^{18}O_P - R^{18}O_R - \frac{K_{O_2}}{Z}\alpha_G(O_2{}^{18}O_{DO} - O_{2sat}{}^{18}O_A\alpha_s)$$

Assuming that the aquatic system is sufficiently large to smooth short duration variations of $^{18}O_{DO}$, $^{18}O_W$, R, K_{O2}, O_2 and α_s, $d^{18}O_{DO}/dt$ tends towards zero. Substituting equation 2 into equation 4 and solving for GPP gives:

$$GPP = \frac{R(^{18}O_{DO} - {}^{18}O_R) + \frac{K_{O_2}}{Z}(O_2 - O_{2sat}) - \frac{K_{O_2}}{Z}\alpha_G(^{18}O_{DO}O_2 - {}^{18}O_AO_{2sat}\alpha_S)}{(^{18}O_{DO} - {}^{18}O_P)} \quad 4.$$

Derivation of Equation 9

The change in the concentration of dissolved inorganic carbon is expressed as:

$$\frac{dDIC}{dt} = R - GPP - \frac{K_{CO_2}}{Z}(CO_2 - CO_{2sat}) \quad 7.$$

Each component of equation 2 is multiplied by its respective isotopic ratio to give the isotope mass balance:

$$\frac{dDIC^{13}C_{DIC}}{dt} = R^{13}C_R - GPP^{13}C_P - \frac{K_{CO_2}}{Z}(CO_2{}^{13}C_{CO_2} - CO_{2sat}{}^{13}C_A) \quad 8.$$

Expanding equation 8 gives:

$$\frac{dDIC}{dt}{}^{13}C_{DIC} + \frac{d^{13}C_{DIC}}{dt}DIC = R^{13}C_R - GPP^{13}C_P - \frac{K_{CO_2}}{Z}(CO_2{}^{13}C_{CO_2} - CO_{2sat}{}^{13}C_A)$$

To simplify equation 8 we assume that the aquatic system is sufficiently large to smooth short duration variations of $^{13}C_{DIC}$, $^{13}C_R$, $^{13}C_{CO2}$, GPP, K_{CO2}, CO_2 and CO_{2sat} so that $d^{13}C_{DIC}/dt$ is equal to zero. By substituting equation 7 into equation 8, equation 8 can be solved for R:

$$R = \frac{GPP(^{13}C_{DIC} - {}^{13}C_P) + \frac{K_{CO_2}}{Z}(CO_2 - CO_{2sat}) - \frac{K_{CO_2}}{Z}(CO_2{}^{13}C_{CO_2} - CO_{2sat}{}^{13}C_A)}{(^{13}C_{DIC} - {}^{13}C_R)} \qquad 9.$$

To solve for GPP and R using the $\delta^{13}C$ method equations 4 and 9 are solved simultaneously by iteration. Concentrations of DO and CO_2 were input in units of mmol m^{-3} and a photosynthetic quotient of 1.0 was used. Using Microsoft Excel this can be done easily using the "solver" tool. Briefly, write the equation 4 in one cell referring to a second cell for R. In this cell write equation 9, referring to a third cell for GPP. This third cell will be the "guess" for R, the value that is solved for by iteration. In a forth cell write a formula for the difference between cell two and three. Using the "solver" tool minimize the difference between R and the guess for R, cells two and three. The "target cell" is cell four and "by changing cells" is cell three.

Error for GPP and R from equations 4 and 9:

To calculate the variance of GPP from equation 4 the superposition of error theorem for calculating variance of a derived variable was used. The variance of the derived variable is equal to the partial derivative of the derived variable with respect to the first variable multiplied by its respective variance plus the partial derivative of the derived variable with

respect to the second variable multiplied by its respective variance. The "parent" variables were considered to be independent so that the covariance term was not included.

$$s_u^2 = \left(\frac{\partial u}{\partial x}\right)^2 s_x^2 + \left(\frac{\partial u}{\partial y}\right)^2 s_y^2 \qquad 10.$$

For GPP calculated from equation 4, equation 4 becomes:

$$s_{GPP}^2 = \left(\frac{\partial GPP}{\partial {}^{18}O_{DO}}\right)^2 s_{{}^{18}O_{DO}}^2 + \left(\frac{\partial GPP}{\partial {}^{18}O_R}\right)^2 s_{{}^{18}O_R}^2 + \left(\frac{\partial GPP}{\partial R}\right)^2 s_R^2 + \left(\frac{\partial GPP}{\partial O_2}\right)^2 s_{O_2}^2 + \left(\frac{\partial GPP}{\partial O_{2sat}}\right)^2 s_{O_{2sat}}^2 + \left(\frac{\partial GPP}{\partial {}^{18}O_P}\right)^2 s_{{}^{18}O_{DO}}^2 \qquad 11.$$

The partial derivatives of each of the parent variables are as follows:

$$\frac{\partial GPP}{\partial {}^{18}O_{DO}} = ({}^{18}O_{DO} - {}^{18}O_P)(R - \frac{K_{O_2}}{Z}\alpha_g) - (R({}^{18}O_{DO} - {}^{18}O_R) + \frac{K_{O_2}}{Z}(O_2 - O_{2sat}) - \frac{K_{O_2}}{Z}\alpha_G(O_2\,{}^{18}O_{DO} - O_{2sat}\,{}^{18}O_A\alpha_S))$$

$$\frac{\partial GPP}{\partial {}^{18}O_R} = \frac{-R}{\delta^{18}O_{DO} - \delta^{18}O_P}$$

$$\frac{\partial GPP}{\partial R} = \frac{\delta^{18}O_{DO} - \delta^{18}O_R}{\delta^{18}O_{DO} - \delta^{18}O_P}$$

$$\frac{\partial GPP}{\partial O_2} = \frac{\frac{K_{O_2}}{Z}(1 - \alpha_g\,{}^{18}O_{DO})}{\delta^{18}O_{DO} - \delta^{18}O_P}$$

$$\frac{\partial GPP}{\partial O_{2sat}} = \frac{\frac{K_{O_2}}{Z}(\alpha_g\alpha_s\,{}^{18}O_A - 1)}{\delta^{18}O_{DO} - \delta^{18}O_P}$$

$$\frac{\partial GPP}{\partial {}^{18}O_P} = R({}^{18}O_{DO} - {}^{18}O_R) + \frac{K_{O_2}}{Z}(O_2 - O_{2sat}) - \frac{K_{O_2}}{Z}\alpha_G(O_2\,{}^{18}O_{DO} - O_{2sat}\,{}^{18}O_A\alpha_S)$$

These partial derivatives were substituted into equation 11 to solve for the variance of GPP. The variances of O_2, O_{2sat}, $^{18}O_{DO}$, $^{18}O_P$ and $^{18}O_R$ were 0.04 mg l^{-1}, 0.04 mg l^{-1}, 0.16‰, 0.01‰ and 0.16‰ respectively, while the variance of R was measured for each case. The standard error is then the square root of the sum of these products. The variance of R from equation 9 was calculated in a like fashion. The variances of CO_2, CO_{2sat}, $^{13}C_{DIC}$ and $^{13}C_{DOC}$, were 0.25 mg l^{-1}, 0.25 mg l^{-1}, 0.04‰ and 0.04‰, respectively.

Confidence intervals of average GPP, R and GPP:R:

The confidence intervals of average GPP, R and GPP:R over the ice-free season or annually are at the α=0.05 critical level. They were calculated as the standard deviation of the measurements divided by the square root of the number of measurements multiplied by the t value at α=0.025 for the appropriate n-1 degrees of freedom:

$$confidence\ \text{int}ervals = \frac{s}{\sqrt{n}} t_{\alpha/2,v};\ v = n-1$$

Appendix 2 Bottle incubation data from lakes Croche and à l'Ours

Table A2- 1 Bottle incubation measurements in Lac Croche between May 2002 and March 2003. Temperature is in °C, length is in hours, photosynthetically available radiation (PAR) is in $\mu E\ m^{-2}\ s^{-1}$ and oxygen concentrations are in $mg\ L^{-1}$.

Lac Croche
23-May
Temperature of incubation 10
Length of incubation for black bottles: 6
Length of incubation for clear bottles: 4

PAR	Replicate Oxygen Concentration			Average [O_2]			SE
initial	10.6934	10.6987	10.6987	10.6969			
946.53	10.6991	10.7020	10.7078	10.7030	GPP	4.42	0.85
398.54	10.7197	10.7212		10.7205	GPP	8.79	0.58
199.27	10.7185	10.7107	10.7219	10.7170	GPP	7.93	1.00
73.07	10.7039	10.7160	10.7041	10.7080	GPP	5.67	1.15
39.85	10.6865	10.6939	10.6928	10.6911	GPP	1.45	0.81
black	10.6803	10.6770	10.6811	10.6795	R	2.91	0.36

20-Jun
Temperature of incubation 17.0
Length of incubation for black bottles: 6.5
Length of incubation for clear bottles: 4

PAR	Replicate Oxygen Concentration			Average [O_2]			SE
initial	9.0847	9.0856	9.0857	9.0853			
946.53	9.1138	9.1058	9.1028	9.1075	GPP	11.28	1.00
481.57	9.1275	9.1227	9.1219	9.1240	GPP	15.41	0.72
215.88	9.1128	9.1174	9.1085	9.1129	GPP	12.63	0.86
111.26	9.1008	9.1008	9.0989	9.1001	GPP	9.45	0.59
48.16	9.0821	9.0790	9.0836	9.0816	GPP	4.80	0.66
black	9.0551	9.0460	9.0429	9.0480	R	5.74	0.57

01-Jul
Temperature of incubation 22.0
Length of incubation for black bottles: 4
Length of incubation for clear bottles: 7

PAR	Replicate Oxygen Concentration				Average [O_2]			SE
initial	7.8925	7.8914	7.8891	7.8962	7.8923			
963.14	7.9479	7.9556	7.9598		7.9544	GPP	19.03	0.80
473.26	7.9644	7.9645			7.9644	GPP	20.46	0.63
232.48	7.9320	7.9374	7.9454		7.9383	GPP	16.73	0.84
106.28	7.9116	7.9183	7.9149		7.9149	GPP	13.39	0.68
53.14	7.8912	7.8846			7.8879	GPP	9.53	0.71
black	7.8481	7.8540	7.8528		7.8517	R	10.16	0.58

15-Jul

Temperature of incubation 22.0

Length of incubation for black bottles: 7.5

Length of incubation for clear bottles: 4

PAR	Replicate Oxygen Concentration				Average [O_2]			
initial	8.1870	8.1769	8.1793	8.1819	8.1812			
929.92	8.2517	8.2456	8.2425		8.2466	GPP	25.78	1.00
464.96	8.2502	8.2528	8.2442		8.2491	GPP	26.40	0.98
215.88	8.2199	8.2237	8.2245		8.2227	GPP	19.81	0.82
120.39	8.2029	8.2007			8.2018	GPP	14.58	0.77
57.29	8.1719	8.1773	8.1765		8.1752	GPP	7.94	0.85
black	8.1109	8.1051	8.1151	8.1107	8.1104	R	9.44	0.40

29-Jul

Temperature of incubation 21.0

Length of incubation for black bottles: 7

Length of incubation for clear bottles: 4

PAR	Replicate Oxygen Concentration				Average [O_2]			
initial	8.1299	8.1288	8.1295	8.1334	8.1304			
763.87	8.1907	8.1903	8.1959		8.1923	GPP	23.88	0.58
431.75	8.2026	8.2042	8.1976		8.2015	GPP	26.18	0.62
224.18	8.1873	8.1958	8.1872		8.1901	GPP	23.33	0.80
107.94	8.1811	8.1627	8.1634		8.1691	GPP	18.07	1.55
58.95	8.1451	8.1361	8.1300		8.1370	GPP	10.07	1.16
black	8.0730	8.0686	8.0708	8.0739	8.0716	R	8.40	0.22

11-Aug

Temperature of incubation 21.0

Length of incubation for black bottles: 7

Length of incubation for clear bottles: 4

PAR	Replicate Oxygen Concentration				Average [O_2]			
initial	8.1690	8.1722	8.1690	8.1672	8.1694			
1062.77	8.2278	8.2357	8.2320		8.2318	GPP	20.63	0.68
489.87	8.2459	8.2426	8.2421		8.2435	GPP	23.55	0.48
182.66	8.2348	8.2291	8.2215		8.2285	GPP	19.79	1.03
86.35	8.2070	8.2008	8.2002		8.2027	GPP	13.34	0.66
39.85	8.1889	8.1803	8.1807		8.1833	GPP	8.50	0.80
black	8.1329	8.1377	8.1335	8.1330	8.1343	R	5.01	0.22

23-Aug

Temperature of incubation 21.0

Length of incubation for black bottles: 7

Length of incubation for clear bottles: 4

PAR	Replicate Oxygen Concentration				Average [O_2]			
initial	8.3099	8.3029	8.3045	8.3053	8.3056			

929.92	8.3539	8.3643	8.3642		8.3608	GPP	17.74	1.06
435.07	8.3772	8.3783			8.3777	GPP	21.98	0.39
219.20	8.3632	8.3681	8.3686		8.3666	GPP	19.20	0.57
111.26	8.3476	8.3466	8.3410		8.3451	GPP	13.82	0.63
44.84	8.3249	8.3210	8.3203		8.3221	GPP	8.07	0.52
black	8.2745	8.2760	8.2832		8.2779	R	3.96	0.44

04-Sep
Temperature of incubation
Length of incubation for black bottles: 7
Length of incubation for clear bottles: 4

PAR	Replicate Oxygen Concentration				Average [O_2]			SE
initial	8.3659	8.3728	8.3647	8.3651	8.3671			
979.74	8.4029	8.4055	8.3981		8.4022	GPP	14.31	0.86
498.17	8.4091	8.4120	8.4061		8.4091	GPP	16.04	0.79
212.55	8.4080	8.4002	8.4048		8.4043	GPP	14.86	0.88
109.60	8.3868	8.3858	8.3825		8.3850	GPP	10.03	0.74
54.80	8.3636	8.3654	8.3671		8.3654	GPP	5.12	0.71
black	8.3330	8.3252	8.3255	8.3292	8.3282	R	5.56	0.38

17-Sep
Temperature of incubation
Length of incubation for black bottles: 7
Length of incubation for clear bottles: 4

PAR	Replicate Oxygen Concentration				Average [O_2]			SE
initial	8.8439	8.8512	8.8440	8.8481	8.8468			
954.83	8.9018	8.9012	8.9011		8.9014	GPP	15.37	0.60
498.17	8.9076	8.9075	8.9209		8.9120	GPP	18.03	1.27
207.57	8.9106	8.9098			8.9102	GPP	17.57	0.61
102.96	8.9033	8.9003	8.8951		8.8996	GPP	14.92	0.85
53.97	8.8850	8.8731	8.8750		8.8777	GPP	9.45	1.10
black	8.8322	8.8341	8.8338	8.8387	8.8347	R	1.73	0.32

01-Oct
Temperature of incubation
Length of incubation for black bottles: 7.5
Length of incubation for clear bottles: 4

PAR	Replicate Oxygen Concentration				Average [O_2]			SE
initial	9.0660	9.0620	9.0622	9.0665	9.0642			
996.35	9.1223	9.1105			9.1164	GPP	13.84	1.18
481.57	9.1469	9.1494	9.1458		9.1474	GPP	21.59	0.61
249.09	9.1534	9.1344	9.1429		9.1436	GPP	20.64	1.48
114.58	9.1356	9.1430	9.1391		9.1392	GPP	19.55	0.77
64.76	9.1065	9.1105	9.1040		9.1070	GPP	11.50	0.73
black	9.0522	9.0618	9.0607		9.0582	R	0.79	0.43

24-Oct
Temperature of incubation
Length of incubation for black bottles: 7.5
Length of incubation for clear bottles: 4

PAR	Replicate Oxygen Concentration				Average [O_2]			
initial	10.6664	10.6574	10.6633	10.6591	10.6616			
996.35	10.6830	10.6752	10.6841		10.6807	GPP	5.41	0.97
452.51	10.7156	10.7142	10.7114		10.7137	GPP	13.66	0.64
207.57	10.7035	10.7171	10.7091		10.7099	GPP	12.70	1.13
107.94	10.7179	10.7094			10.7136	GPP	13.63	0.93
61.44	10.7056	10.6928			10.6992	GPP	10.03	1.26
black	10.6542	10.6598	10.6578	10.6560	10.6569	R	0.61	0.32

06-Nov
Temperature of incubation
Length of incubation for black bottles: 6.83

PAR	Replicate Oxygen Concentration				Average [O_2]			
initial	11.8514	11.8666	11.8612	11.8578	11.8593			
black	11.8557	11.8518	11.8509	11.8490	11.8519	R	1.08	0.51

Table A2- 2 Bottle incubation measurements in Lac à l'Ours between May 2002 and March 2003. Temperature is in °C, length is in hours, photosynthetically available radiation (PAR) is in μE m^{-2} s^{-1} and oxygen concentrations are in mg L^{-1}.

Lac a l'Ours
23-May
Temperature of incubation 10
Length of incubation for black bottles: 4
Length of incubation for clear bottles: 4

PAR	Replicate Oxygen Concentration				Average [O_2]			
initial	10.6838	10.6840	10.6835	10.6836	10.6838			
1062.77	10.7477	10.7382	10.7436		10.7432	GPP	18.08	0.69
464.96	10.7814	10.7756			10.7785	GPP	26.91	0.51
199.27	10.7708	10.7729	10.7601		10.7679	GPP	24.27	0.99
83.03	10.7415	10.7418	10.7492		10.7442	GPP	18.33	0.63
46.50	10.7079	10.7033			10.7056	GPP	8.69	0.41
black	10.6708	10.6709	10.6710		10.6709	R	3.23	0.03

04-Jun
Temperature of incubation 15
Length of incubation for black bottles: 6
Length of incubation for clear bottles: 4

PAR	Replicate Oxygen Concentration				Average [O_2]			
initial	9.5896	9.5878	9.5949	9.5937	9.5915			
1037.86	9.7232	9.7225	9.7234		9.7230	GPP	45.15	0.08
415.14	9.7640	9.7649	9.7703		9.7664	GPP	55.99	0.50
230.82	9.7198	9.7289	9.7151		9.7213	GPP	44.72	1.02
97.97	9.6762	9.6705			9.6733	GPP	32.73	0.51
43.18	9.6204	9.6123	9.6180		9.6169	GPP	18.62	0.60
black	9.5249	9.5194	9.5140	9.5132	9.5179	R	12.28	0.53

20-Jun

Temperature of incubation 20.0

Length of incubation for black bottles: 7.25

Length of incubation for clear bottles: 4

PAR	Replicate Oxygen Concentration			Average [O_2]			
initial	8.4395	8.4308	8.4359	8.4352			
1029.56	8.5039	8.5074		8.5056	GPP	31.62	1.16
464.96	8.5247	8.5249		8.5248	GPP	36.41	1.12
215.88	8.5099	8.4943	8.4838	8.4960	GPP	29.21	2.20
96.31	8.4348	8.4537	8.4447	8.4444	GPP	16.30	1.76
53.14	8.3807	8.4209		8.4008	GPP	5.41	3.72
black	8.3397	8.3213	8.3400	8.3337	R	14.00	0.92

03-Jul

Temperature of incubation 26.0

Length of incubation for black bottles: 7.5

Length of incubation for clear bottles: 4

PAR	Replicate Oxygen Concentration			Average [O_2]			
initial	7.2055	7.2069	7.2003	7.2042			
896.71	7.3416	7.3539	7.3293	7.3416	GPP	51.14	1.87
514.78	7.4051	7.3958	7.3964	7.3991	GPP	65.53	0.96
214.21	7.3330	7.3316		7.3323	GPP	48.82	0.61
119.56	7.2607	7.2594		7.2601	GPP	30.77	0.61
61.44	7.1911	7.1932	7.1953	7.1932	GPP	14.05	0.67
black	7.0796	7.0767		7.0781	R	16.81	0.33

17-Jul

Temperature of incubation 21.0

Length of incubation for black bottles: 7.5

Length of incubation for clear bottles: 4

PAR	Replicate Oxygen Concentration			Average [O_2]			
initial	8.2379	8.2356	8.2451	8.2395			
963.14	8.4049	8.4049		8.4049	GPP	56.28	0.82
456.66	8.4308	8.4302		8.4305	GPP	62.68	0.82
224.18	8.3933	8.4002	8.3944	8.3960	GPP	54.04	0.98
100.46	8.2910	8.2895		8.2903	GPP	27.62	0.83
61.44	8.2309	8.2427		8.2368	GPP	14.24	1.33
black	8.1274	8.1291	8.1261	8.1275	R	14.93	0.40

31-Jul
Temperature of incubation 24.0
Length of incubation for black bottles: 6.83
Length of incubation for clear bottles: 4

PAR	Replicate Oxygen Concentration				Average [O_2]			SE
initial	7.6907	7.6934	7.6863		7.6901			
589.51	7.9000	7.9099	7.9119		7.9073	GPP	64.35	1.16
298.90	7.9222	7.9331	7.9279		7.9277	GPP	69.46	1.06
114.58	7.8456	7.8583	7.8550		7.8530	GPP	50.77	1.19
56.46	7.7552	7.7645			7.7598	GPP	27.48	1.08
31.88	7.7092	7.7081	7.7040		7.7071	GPP	14.30	0.81
black	7.6172	7.6213	7.6186	7.6286	7.6214	R	10.06	0.48

23-Aug
Temperature of incubation 21.0
Length of incubation for black bottles: 7
Length of incubation for clear bottles: 4

PAR	Replicate Oxygen Concentration				Average [O_2]			SE
initial	8.1831	8.1807	8.1744		8.1794			
929.92	8.2880	8.2918			8.2899	GPP	38.58	0.90
435.07	8.3392	8.3377	8.3326		8.3365	GPP	50.23	0.98
219.20	8.3133	8.2976	8.3071		8.3060	GPP	42.60	1.42
111.26	8.2404	8.2427			8.2415	GPP	26.49	0.87
44.84	8.2042	8.1953	8.1872		8.1956	GPP	15.00	1.48
black	8.1029	8.1104	8.0998	8.0978	8.1027	R	10.96	0.54

04-Sep
Temperature of incubation 21.0
Length of incubation for black bottles: 7
Length of incubation for clear bottles: 4

PAR	Replicate Oxygen Concentration			Average [O_2]			SE
initial	8.2631	8.2634	8.2679	8.2648			
1062.77	8.4569	8.4486		8.4527	GPP	57.64	1.17
489.87	8.4787	8.4555	8.4664	8.4669	GPP	61.18	1.91
182.66	8.4106	8.4018	8.4231	8.4118	GPP	47.42	1.79
86.35	8.3250	8.3684		8.3467	GPP	31.13	3.94
39.85	8.2822	8.2783	8.2777	8.2794	GPP	14.31	0.98
black	8.1805	8.1999	8.1901	8.1902	R	10.66	0.83

17-Sep
Temperature of incubation
Length of incubation for black bottles: 7
Length of incubation for clear bottles: 4

PAR	Replicate Oxygen Concentration			Average [O_2]	SE
initial	8.7906	8.7932	8.7933	8.7924	

896.71	8.9801	8.9720	8.9728	8.9750	GPP	55.55	1.53
456.66	8.9854	8.9974	8.9764	8.9864	GPP	58.41	2.06
185.98	8.9774	8.9659		8.9716	GPP	54.72	1.72
99.63	8.9099	8.9188	8.9057	8.9114	GPP	39.67	1.69
51.48	8.8329	8.8499	8.8477	8.8435	GPP	22.69	1.93
black	8.7135	8.7326		8.7230	R	9.91	1.37

01-Oct

Temperature of incubation 16.0

Length of incubation for black bottles: 7.25

Length of incubation for clear bottles: 4

PAR	Replicate Oxygen Concentration			Average [O_2]			SE
initial	8.6828	8.6963	8.6862	8.6885			
1012.95	8.8168	8.8255		8.8211	GPP	39.31	1.51
481.57	8.8415	8.8511	8.8448	8.8458	GPP	45.47	1.47
207.57	8.8524	8.8270	8.8368	8.8387	GPP	43.71	2.26
96.31	8.8160	8.7977	8.8093	8.8077	GPP	35.94	1.86
56.46	8.7705	8.7671	8.7629	8.7668	GPP	25.73	1.41
black	8.6512	8.6445	8.6362	8.6440	R	6.13	0.82

24-Oct

Temperature of incubation 7.0

Length of incubation for black bottles: 7.69

Length of incubation for clear bottles: 4

PAR	Replicate Oxygen Concentration				Average [O_2]			SE
initial	10.6963	10.6875	10.6818	10.6780	10.6859			
946.53	10.6978	10.6949	10.6902		10.6943	GPP	4.50	1.39
473.26	10.7685	10.7721	10.7696		10.7701	GPP	23.44	1.33
207.57	10.7749	10.7701	10.7698		10.7716	GPP	23.82	1.36
109.60	10.7624	10.7667			10.7645	GPP	22.05	1.35
58.12	10.7341	10.7282	10.7314		10.7312	GPP	13.73	1.37
black	10.6708	10.6683	10.6654	10.6653	10.6675	R	2.40	0.54

06-Nov

Temperature of incubation 4.0

Length of incubation for black bottles: 6.83

PAR	Replicate Oxygen Concentration				Average [O_2]			SE
initial	10.9170	10.9277	10.9133	10.9205	10.9196			
black	10.9169	10.9236		10.9198	10.9201	R	-0.06	0.59

04-Dec

Temperature of incubation 1.0

Length of incubation for black bottles: 6

PAR	Replicate Oxygen Concentration				Average [O_2]			
initial	12.5706	12.5617	12.5768		12.5697			
black	12.5683	12.5993	12.5687	12.5764	12.5782	R	-1.41	1.37

05-Feb

Temperature of incubation 3.0

Length of incubation for black bottles: 7.33

PAR	Replicate Oxygen Concentration				Average [O_2]			
initial	11.0364	11.0396	11.0379	11.0365	11.0376			
black	11.0455	11.0500	11.0529	11.0507	11.0498	R	-1.66	0.24

26-Feb

Temperature of incubation 3.0

Length of incubation for black bottles: 7.35

PAR	Replicate Oxygen Concentration				Average [O2]			
initial	11.0364	11.0253	11.0381		11.0332			
black	11.0163	11.0362	11.0270	11.0173	11.0242	R	1.23	0.79

19-Mar

Temperature of incubation 3.0

Length of incubation for black bottles: 6.75

PAR	Replicate Oxygen Concentration				Average [O2]			
initial	10.3767	10.3831	10.3811		10.3803			
black	10.3852	10.3803	10.3767		10.3807	R	-0.06	0.46

Appendix 3 Temperature and oxygen profiles from lakes Croche and à l'Ours

Table A3- 3 Temperature profiles in Lac Croche between May 2002 and March 2003. Depth of mixed layer (e_z) is shown in meters for the stratified period and ice thickness is shown in cm for the ice-covered period.

Depth	22-May	27-May	03-Jun	10-Jun	20-Jun	26-Jun	01-Jul	08-Jul	15-Jul	23-Jul	29-Jul	07-Aug	11-Aug	23-Aug	03-Sep	11-Sep	17-Sep	24-Sep
0	10.4	14	14.4	17.0	18.0	19.9	24.3	23.1	22.4	22.9	24.3	21.4	22.5	21.5	21.0	21.8	18.4	18.0
-0.5	10.2	13.9	14.4	17.0	17.8	19.8	24.2	23.0	22.4	22.9	24.3	21.4	22.5	21.6	21.0	21.8	18.4	18.0
-1	10.2	13.8	14.4	17.0	17.4	19.8	24.0	23.0	22.4	22.9	24.3	21.4	22.5	21.6	21.0	21.8	18.4	18.0
-1.5	10.2	13.7	14.3	16.9	16.6	19.7	23.6	23.0	22.4	22.9	23.9	21.4	22.4	21.6	21.0	21.8	18.4	18.0
-2	10.1	13.2	14.3	16.9	16.2	19.5	21.7	23.0	22.4	22.9	23.3	21.4	22.3	21.6	21.0	21.8	18.4	18.0
-2.5	10.0	12.5	14.2	16.9	16.0	17.8	19.4	22.8	22.0	22.5	22.3	21.4	21.9	21.6	20.9	21.8	18.4	18.0
-3	9.6	11.6	14.1	15.2	15.6	16.7	17.7	19.0	21.1	21.5	22.0	21.4	21.7	21.5	20.8	21.5	18.4	18.0
-3.5	9.2	11.2	11.5	13.4	14.4	15.1	15.9	16.8	18.4	18.9	20.9	21.3	21.3	21.5	20.7	20.4	18.4	18.0
-4	8.8	9.8	10.1	11.5	13.0	13.3	14.5	14.9	15.1	16.2	19.4	21.2	19.8	20.9	20.3	19.9	18.4	18.0
-4.5	8.6	9.2	9.4	10.7	11.9	11.8	12.7	12.8	13.8	13.5	16.2	16.3	16.8	17.7	18.8	19.0	18.4	17.9
-5	8.3	8.7	8.7	9.4	10.0	10.6	11.0	11.1	12.0	11.9	14.3	14.0	14.2	15.1	16.1	16.9	17.7	17.5
-5.5	8.0	8.2	8.0	8.7	8.9	9.3	9.6	9.9	11.2	10.7	12.4	12.2	12.4	13.2	14.1	14.4	15.0	15.3
-6	7.4	7.4	7.3	7.8	8.2	8.7	8.6	8.8	9.5	9.2	11.2	10.7	10.9	11.3	12.0	12.7	12.7	13.6
-6.5	7.0	7.0	7.0	7.4	7.5	7.9	8.0	8.2	8.8	8.2	9.4	9.8	9.6	10.2	10.6	11.3	11.5	11.6
-7	6.4	6.4	6.7	6.8	7.2	7.5	7.6	7.6	8.1	7.4	8.7	8.9	8.9	9.1	9.7	10	10.2	10.3
-7.5	6.0	6.3	6.5	6.6	6.8	7.1	7.1	7.4	7.7	7.0	8.0	8.0	8.0	8.3	8.7	8.7	9.2	9.4
-8	6.0	6.0	6.3	6.4	6.6	6.8	6.9	7.1	7.2	6.5	7.7	7.6	7.7	7.8	8.1	8.2	8.4	8.9
-8.5	5.9	6.0	6.1	6.3	6.5	6.6	6.8	6.9	7.1	6.4	7.3	7.3	7.3	7.5	7.7	8.0	8.1	8.2
-9	5.8	5.8			6.3	6.5	6.8			6.3	7.1	7.1	7.2					
e_z	**3.3**	**3.3**	**3.3**	**3.3**	**3.0**	**2.3**	**2.5**	**2.8**	**3.0**	**3.0**	**3.5**	**4.3**	**4.0**	**4.0**	**4.3**	**4.8**	**4.8**	**5.0**

Depth	01-Oct	09-Oct	15-Oct	23-Oct	30-Oct	06-Nov	13-Nov	04-Dec	11-Dec	Dec-18	Jan-09	Jan-15	Jan-21	Jan-29	Feb-05	Feb-12	Feb-26	13-Mar	19-Mar
0	15.4	13.2	11.1	8.3	6.1	3.4	4.0	ice	ice	ice	ice	ice	ice	ice	ice	ice	ice	ice	Ice
-0.5	15.9	13.2	11.2	8.3	6.1	3.6	4.0	2.1	1.8	0.8	1.4	1.3							
-1	15.9	13.2	11.2	8.3	6.1	3.7	4.0	2.3	2.1	1.5	2.4	1.8	1.1	1.2	1.3	1.1	0.3	2.0	0.6
-1.5	15.9	13.2	11.2	8.3	6.1	3.8	4.0	2.4	2.4	2.4	2.7	2.6							
-2	15.9	13.2	11.2	8.3	6.1	3.9	4.0	2.5	2.6	2.6	2.9	2.9	2.5	2.7	2.4	2.5	2.5	2.6	2.6
-2.5	15.9	13.2	11.2	8.3	6.1	3.8	4.0	2.7	2.7	2.9	3.1	3.2							
-3	15.9	13.2	11.2	8.3	6.1	3.8	4.0	2.8	3.0	3.1	3.5	3.4	3.3	3.5	3.4	3.5	3.7	3.8	3.7
-3.5	15.9	13.2	11.2	8.3	6.1	3.8	4.0	3.0	3.2	3.3	3.6	3.6							
-4	15.9	13.2	11.2	8.3	6.1	3.9	4.0	3.2	3.4	3.5	3.8	3.9	3.8	3.9	3.9	3.9	4.0	4.0	4.0
-4.5	15.9	13.2	11.2	8.3	6.1	3.9	4.0	3.4	3.5	3.6	3.9	4.0							
-5	15.9	13.2	11.2	8.3	6.1	3.9	4.0	3.6	3.6	3.7	4.0	4.0	3.9	4.1	4.0	4.1	4.0	4.1	4.1
-5.5	15.8	13.2	11.2	8.3	6.1	3.9	4.0	3.7	3.7	3.8	4.0	4.1							
-6	14.2	13.2	11.2	8.2	6.1	4.0	4.0	3.7	3.8	3.9	4.0	4.1	4.0	4.1	4.1	4.1	4.1	4.2	4.1
-6.5	12.5	13.2	11.2	8.2	6.1	4.0	4.0	3.8	3.9	4.0	4.1	4.2							
-7	10.8	11.7	11.2	8.2	6.1	4.0	4.0	3.9	4.0	4.0	4.2	4.2	4.2	4.2	4.2	4.2	4.2	4.3	4.1
-7.5	9.7	9.9	11.1	8.2	6.1	4.0	4.0	3.9	4.0	4.0	4.2	4.3							
-8	8.7	8.8	9.9	8.2	6.1	4.0	4.0	4.0	4.1	4.1	4.3	4.4	4.3	4.3	4.3	4.3	4.3	4.4	4.2
-8.5	8.3	8.6	8.5	8.2	6.1	4.0	4.1	4.1	4.3	4.1	4.3	4.4							
								Ice thickness											
e_z	**5.8**	**6.8**	**7.8**	**8.0**	**8.0**	**8.0**	**8.0**	**15.0**	**15.0**	**30.0**	**28.8**	**38.0**	**38.0**	**39.0**	**38.8**	**51.0**	**51.3**	**52.5**	**62.5**

Table A3- 4. Temperature profiles for Lac à l'Ours between May 2002 and March 2003. Depth of mixed layer (e_z) is shown in meters for the stratified period and ice thickness is shown in cm for the ice-covered period.

Depth	23-May	29-May	04-Jun	11-Jun	21-Jun	27-Jun	03-Jul	10-Jul	17-Jul	25-Jul	31-Jul	08-Aug	13-Aug	24-Aug	30-Aug	04-Sep	12-Sep	18-Sep	26-Sep
0	9.3	15.6	15.4	17.7	20.4	21.3	28	22.4	21.6	22.2	24.0	21.1	24.6	20.8	20.4	20.8	19.2	17.9	17.6
-0.5	9.2	15.4	15.4	17.7	20.3	21.3	27.8	22.4	21.8	22.3	24.0	21.1	24.7	20.9	20.4	20.9	19.2	17.9	17.6
-1	9.1	14.8	15.4	17.7	19.6	21.3	27.4	22.4	21.8	22.2	24.0	21.1	24.7	20.9	20.4	20.9	19.2	17.9	17.5
-1.5	9.0	13.8	15.4	17.7	17.6	21.3	24.4	22.4	21.8	22.2	24.0	21.1	24.6	20.9	20.4	20.9	19.2	17.9	17.5
-2	9.0	13.1	15.2	17.7	16.2	17.0	18.1	21.6	21.8	22.2	23.3	21.1	22.9	20.9	20.4	20.7	19.2	17.9	17.4
-2.5	9.0	12.7	14.8	16.1	15.5	15.7	16.5	17.4	19.7	22.1	21.7	20.9	20.9	20.9	20.5	20.3	19.2	17.9	17.4
-3	8.9	12	13.9	14.1	14.9	14.5	14.1	14.4	16.2	21.2	18.6	18.3	18.1	18.5	19.1	19.9	19.1	17.9	17.4
-3.5	8.8	11.4	12	12.7	14.4	13.2	13.2	12.9	13.7	20.8	15.6	15.0	15.2	16.0	16.3	17.2	17.3	17.6	17.2
-4	8.7	10.5	10.8	11.5	11.7	11.7	11.3	11.4	11.7	19.5	13.1	12.6	12.9	13.1	13.2	14.9	14.6	14.8	15.2
-4.5	8.6	9.9	10.1	10.4	10.6	10.6	10.4	10.6	11.1	16.5	11.5	11.1	11.3	11.6	11.8	12.1	11.3	12.3	13.0
-5	8.3	9.2	9.4	9.5	9.8	9.4	9.3	9.5	9.8	15.1	10.7	10.1	10	9.9	10.5	10.6	10.3	10.9	11.4
-5.5	8.1	8.7	8.8	8.9	9.0	8.9	8.7	8.9	9.3	14.5	9.5	9.0	9.2	9.1	9.4	9.6	9.5	9.9	10.0
-6	7.9	8.2	8.0	8.3	8.2	8.5	8.0	8.2	8.2	11.9	8.8	8.3	8.2	8.4	8.4	8.7	8.5	8.6	9.1
-6.5	7.7	7.9	7.6	8.0	8.0	7.9	7.9	7.7	8.1	10.8	8.1	7.8	7.8	8.0	7.9	8.3	7.9	8.1	8.2
-7	7.5	7.5	7.4	7.5	7.5	7.5	7.4	7.2	7.4	9.9	7.7	7.5	7.3	7.3	7.2	7.8	7.4	7.5	7.6
-7.5	7.3	7.3	7.3	7.2	7.2	7.3	7.2	7.0	7.2	9.4	7.2	7.1	7.1	7.1	7.0	7.2	7.2	7.2	7.2
-8	7.2	6.8	7.0	7.0	6.8	6.9	6.8	6.6	6.7	8.8	6.9	6.9	6.8	6.9	6.7	7.1	6.9	6.9	6.9
-8.5	7.1	6.7	6.8	6.8	6.6	6.8	6.7	6.5	6.6	8.5	6.7	6.7	6.6	6.7	6.6		6.7	6.7	6.7
-9	7.0	6.5	6.5	6.6	6.3	6.6	6.5	6.3	6.4	8.3	6.6	6.5	6.4	6.6	6.4		6.5	6.5	6.5
-9.5	6.6	6.3	6.4	6.5	6.2	6.4	6.4	6.2	6.3		6.5	6.3	6.3	6.4	6.3		6.4	6.4	6.3
-10	6.1	6.1	6.2	6.3	5.7	6.4	6.3	6.0	6.1		6.4	6.1	6.2	6.0	6.1		6.3	6.3	6.2
-10.5	5.7	6.0	6.2	6.1	5.7	6.3	6.2	5.9	6.0		6.4	6.0	6.0	5.9	6.0		6.2	6.0	6.1
-11	5.5	5.9	6.1	5.9	5.8	6.1	6.1	5.8	5.8			5.9	6.0	5.8	5.8		6.1	5.9	
-11.5		5.8	6	5.8		5.8	6.0	5.8	5.8			5.8	5.9	5.8	5.8		5.9	5.8	
-12		5.7	5.9	5.7			5.9		5.7				5.9		5.7		5.8		
-12.5		5.6		5.6			5.8		5.7				5.8		5.7				
e_z	**4.8**	**3.5**	**2.8**	**2.3**	**2.3**	**2.3**	**2.3**	**2.3**	**2.5**	**2.8**	**2.8**	**2.8**	**2.8**	**2.8**	**2.8**	**3.0**	**3.3**	**3.8**	**3.8**

Depth	02-Oct	11-Oct	17-Oct	24-Oct	31-Oct	07-Nov	14-Nov	04-Dec	11-Dec	18-Dec	Jan-09	Jan-15	Jan-21	Jan-29	Feb-05	Feb-12	Feb-26	13-Mar	19-Mar
0	16.2	11.9	9.6	7.3	3.7	0.2	3.6		ice	ice	ice	ice	ice	ice	ice	ice	ice	ice	ice
-0.5	16.2	11.9	9.7	7.4	5.5	3.1	3.5	1.9	1.4	0.8	0.4	0.9							
-1	16.2	11.9	9.7	7.4	5.5	3.2	3.6	2.3	2.0	1.8	1.3	1.7	1.7	0.8	1.0	0.8	0.9	0.5	0.5
-1.5	16.1	11.9	9.7	7.4	5.5	3.1	3.7	2.4	2.3	2.2	1.9	2.2							
-2	16.1	11.9	9.7	7.4	5.5	3.1	3.8	2.4	2.4	2.3	2.2	2.3	2.1	2.0	2.0	2.0	1.8	2.0	1.8
-2.5	16.0	11.9	9.7	7.4	5.5	3.1	3.8	2.4	2.4	2.4	2.4	2.4							
-3	15.9	11.9	9.7	7.4	5.5	3.1	3.8	2.4	2.4	2.4	2.5	2.5	2.5	2.5	2.5	2.5	2.5	2.4	2.5
-3.5	15.9	11.9	9.7	7.4	5.5	3.1	3.8	2.4	2.5	2.5	2.6	2.6							
-4	15.2	11.9	9.7	7.4	5.5	3.1	3.8	2.4	2.5	2.5	2.6	2.7	2.6	2.7	2.7	2.7	2.7	2.8	2.7
-4.5	14.2	11.9	9.6	7.4	5.5	3.1	3.8	2.4	2.5	2.6	2.7	2.7							
-5	12.2	11.9	9.6	7.4	5.5	3.1	3.8	2.5	2.6	2.6	2.7	2.8	2.7	2.8	2,8	2.8	2.9	2.9	3.0
-5.5	10.5	11.8	9.6	7.4	5.5	3.1	3.8	2.5	2.6	2.6	2.8	2.8							
-6	9.0	10.6	9.6	7.4	5.5	3.1	3.8	2.5	2.6	2.7	2.8	2.8	2.8	2.9	2.9	2.9	3.0	3.0	3.0
-6.5	8.4	8.5	9.6	7.4	5.5	3.1	3.8	2.5	2.6	2.7	2.8	2.9							
-7	7.9	8.0	9.4	7.3	5.5	3.1	3.8	2.6	2.6	2.7	2.8	2.9	2.9	3.0	3.0	3.0	3.0	3.0	3.1
-7.5	7.6	7.6	8.7	7.3	5.5	3.1	3.8	2.6	2.6	2.7	2.9	3.0							
-8	7.5	7.2	7.0	7.3	5.5	3.1	3.8	2.6	2.7	2.8	2.9	3.0	3.0	3.0	3.0	3.0	3.0	3.1	3.1
-8.5		6.9	6.8	7.2	5.5	3.1	3.8	2.7	2.7	2.8	3.0	3.0							
-9		6.7	6.7	7.1	5.5	3.1	3.8	2.7	2.8	2.8	3.0	3.0	3.0	3.0	3.1	3	3.1	3.1	3.1
-9.5		6.5	6.6	7.0				2.7	2.8	2.9	3.0	3.1							
-10		6.4	6.5	6.4				2.7	2.8	2.9	3.1	3.1	3.1	3.1	3.1	3.1	3.1	3.1	3.1
-10.5		6.3		6.3				2.8	2.8	2.9	3.1	3.1							
-11		6.1						2.8		3.0	3.1	3.1	3.1	3.1	3.1	3.1	3.2	3.2	3.2
-11.5								2.8		3.0	3.1	3.1							
-12										3.1	3.2	3.2	3.1	3.2	3.2	3.2	3.2	3.2	3.3
-12.5										3.2	3.2	3.2							
-13										3.2	3.2		3.2	3.3	3.3	3.3	3.3	3.3	3.3
										3.2	3.2								
e_z	**4.0**	**5.8**	**7.3**	**9.5**	**10.5**	Ice thickness		**15.0**	**17.5**	**22.5**	**33.8**	**45.0**	**45.0**	**45.0**	**46.0**	**53.0**	**53.8**	**72.5**	**72.0**

Table A3- 5. Oxygen profiles (mg O_2 L^{-1}) in Lac Croche between May 2002 and March 2003.

Depth	23-May	27-May	3-Jun	10-Jun	20-Jun	26-Jun	1-Jul	8-Jul	15-Jul	31-Jul	7-Aug	11-Aug	23-Aug	3-Sep	13-Sep	17-Sep	24-Sep
0.0	10.60	9.80	9.71	9.22	9.11	8.72	7.83	8.22	8.31	8.06	8.46	8.28	8.46	8.53	8.40	8.98	9.05
0.5	10.70	9.70	9.72	9.19	9.14	8.68	7.86	8.21	8.30	8.11	8.46	8.29	8.42	8.51	8.37	8.92	9.04
1.0	10.80	9.80	9.74	9.17	9.22	8.64	7.89	8.21	8.26	8.11	8.40	8.27	8.41	8.49	8.38	8.90	9.03
1.5	10.85	9.77	9.72	9.16	9.26	8.66	7.80	8.20	8.25	8.00	8.44	8.24	8.39	8.48	8.38	8.90	9.00
2.0	10.90	9.84	9.73	9.14	9.25	8.85	8.62	8.17	8.22	7.95	8.38	8.23	8.37	8.46	8.38	8.89	9.00
2.5	10.90	10.11	9.72	9.07	9.20	9.34	9.14	8.13	8.38	8.22	8.38	8.40	8.35	8.43	8.38	8.87	9.02
3.0	10.90	10.29	9.72	9.72	9.20	9.35	9.23	9.73	8.33	8.00	8.38	8.31	8.34	8.43	8.34	8.86	9.01
3.5	11.00	10.27	11.16	10.56	10.10	9.81	9.55	10.24	9.82	8.30	8.39	8.26	8.31	8.37	8.47	8.85	9.01
4.0	11.10	10.71	11.39	10.88	10.69	10.45	10.08	10.77	10.77	9.95	8.36	9.10	8.65	8.43	8.43	8.84	9.00
4.5	11.10	10.79	11.42	10.89	10.80	10.53	10.17	10.63	10.80	11.05	11.38	10.74	10.77	9.88	8.81	8.82	9.00
5.0	11.10	10.75	11.21	10.78	10.61	10.24	10.03	9.89	10.32	11.95	12.38	11.59	11.44	10.40	9.22	8.50	8.22
5.5	11.00	10.55	10.76	10.53	10.19	9.63	9.32	9.23	9.64	11.33	11.26	10.60	10.28	8.17	7.13	6.14	5.23
6.0	10.90	9.88	9.85	9.18	9.42	8.33	8.40	8.46	8.10	7.39	7.56	8.19	5.94	5.07	4.33	3.01	2.94
6.5	10.10	9.03	9.18	8.50	8.04	7.85	6.87	6.89	6.65	5.22	4.63	3.44	2.37	1.90	1.73	1.18	0.52
7.0	9.30	8.11	8.69	7.65	7.00	6.60	5.94	5.59	5.01	3.73	2.70	1.70	0.83	0.37	0.30	0.30	0.27
7.5	8.75	7.52	7.87	6.55	5.35	5.50	3.98	3.54	2.87	2.30	1.28	0.85	0.29	0.22	0.25	0.21	0.25
8.0	8.20	7.10	7.03	5.43	4.16	4.18	3.06	2.46	1.88	1.40	0.22	0.23	0.27	0.19	0.22	0.26	0.25
8.5	6.35	6.87	6.18	5.11	3.69	2.99	2.87	1.73	1.04	0.21	0.16	0.21	0.27	0.19	0.22	0.25	0.24
9.0	4.50	4.50	6.18	5.11	3.69	2.99	2.87	1.73	1.04	0.17	0.15	0.20	0.27	0.00	0.00	0.00	0.00

Depth	1-Oct	9-Oct	15-Oct	24-Oct	30-Oct	6-Nov	13-Nov	11-Dec	18-Dec	9-Jan	15-Jan	29-Jan	5-Feb	12-Feb	26-Feb	13-Mar	19-Mar
0.0	9.78	10.04	10.51	11.26	11.91	12.46	12.52	ice	ice	ice	ice	ice	ice	ice	ice	ice	ice
0.5	8.61	10.01	10.45	11.22	11.85	12.16	12.54	11.95	12.51	12.47	11.78	ice	ice	ice	ice	ice	ice
1.0	8.59	9.99	10.43	11.20	11.82	12.06	12.50	12.23	12.57	11.82	11.28	11.47	11.39	11.50	10.82	10.41	10.48
1.5	8.58	9.98	10.39	11.19	11.78	12.00	12.51	12.02	12.38	11.58	10.83						
2.0	8.57	9.93	10.38	11.17	11.77	11.94	12.47	11.74	12.00	11.36	10.41	10.56	10.42	10.54	9.93	9.89	9.80
2.5	8.57	9.94	10.37	11.15	11.76	11.90	12.47	11.58	11.65	11.05	10.01						
3.0	8.56	9.91	10.37	11.14	11.74	11.92	12.47	11.23	11.45	10.37	9.63	9.58	9.44	9.26	7.16	7.50	7.26
3.5	8.56	9.91	10.35	11.14	11.75	11.85	12.46	11.04	11.16	10.08	9.24						
4.0	8.55	9.91	10.33	11.12	11.73	11.85	12.46	10.79	10.90	9.65	8.67	8.52	7.95	7.66	6.75	6.51	6.54
4.5	8.55	9.87	10.33	11.12	11.72	11.85	12.46	10.46	10.76	9.25	8.32						
5.0	8.49	9.88	10.33	11.10	11.70	11.85	12.45	10.30	10.32	8.92	8.01	7.67	7.59	7.38	6.63	6.20	6.11
5.5	7.92	9.86	10.33	11.09	11.70	11.82	12.44	10.02	10.13	8.67	7.64						
6.0	2.69	9.85	10.28	11.06	11.68	11.81	12.41	9.80	9.92	8.34	7.40	7.47	7.24	7.38	6.53	5.10	5.99
6.5	0.95	9.85	10.28	11.07	11.68	11.79	12.41	9.66	9.67	7.85	6.78						
7.0	0.23	1.93	10.23	11.07	11.67	11.80	12.40	9.38	9.34	7.26	5.73	6.56	5.34	6.04	5.35	3.28	5.72
7.5	0.22	0.35	10.18	11.07	11.67	11.77	12.38	8.98	8.95	6.40	4.66						
8.0	0.21	0.32	1.18	11.08	11.65	11.77	12.36	7.59	8.35	5.01	3.40	3.95	3.84	4.24	2.57	1.32	4.13
8.5	0.21	0.31	0.28	11.08	11.64	11.72	11.88	0.32	7.06								
9.0	0.00	0.00	0.00	11.08													

Table A3- 6. Oxygen profiles (mg O_2 L^{-1}) in Lac à l'Ours between May 2002 and March 2003.

Depth	29-May	04-Jun	11-Jun	21-Jun	27-Jun	03-Jul	10-Jul	17-Jul	31-Jul	08-Aug	13-Aug	24-Aug	30-Aug	12-Sep	18-Sep	26-Sep
0	9.53	9.58	9.13	8.60	8.49	7.46	8.31	8.43	8.06	8.51	7.97	8.57	8.65	8.82	9.08	9.13
0.5	9.45	9.55	9.04	8.57	8.47	7.52	8.28	8.11	8.06	8.51	7.97	8.56	8.60	8.78	9.04	9.13
1	9.86	9.53	9.04	8.96	8.46	7.31	8.25	8.07	8.04	8.44	7.94	8.52	8.60	8.74	9.04	9.21
1.5	9.82	9.50	9.04	9.32	8.44	8.99	8.23	8.06	8.03	8.42	7.94	8.47	8.57	8.71	9.01	9.27
2	9.81	9.47	9.03	9.19	9.28	9.19	9.26	7.96	8.01	8.38	8.26	8.46	8.55	8.69	8.99	9.29
2.5	9.57	9.49	9.07	8.85	8.61	8.16	8.84	8.47	6.96	8.21	7.58	8.37	8.54	8.68	8.97	9.31
3	9.42	9.55	8.88	8.43	7.78	7.15	7.14	7.13	6.75	5.75	4.93	4.32	4.46	8.45	8.93	9.33
3.5	9.38	9.40	8.66	7.80	7.27	6.84	6.31	5.87	4.79	4.25	3.31	2.54	2.00	2.10	5.83	8.64
4	9.01	8.87	8.30	7.30	6.79	5.85	5.84	4.75	4.34	3.15	2.53	2.05	1.58	0.56	0.29	0.30
4.5	9.06	8.72	7.80	6.90	6.63	5.61	4.74	4.27	3.87	3.03	2.50	2.11	1.30	0.84	0.32	0.28
5	8.73	8.43	7.42	6.61	6.21	5.74	5.33	4.62	3.79	3.45	2.83	2.52	1.43	0.98	0.56	0.28
5.5	8.61	8.34	7.47	6.72	6.29	5.70	5.36	4.62	4.04	3.62	3.25	2.33	1.76	1.00	1.16	0.49
6	8.53	8.25	7.53	6.79	6.34	5.69	5.56	4.46	3.87	3.72	2.86	2.36	2.24	1.12	1.12	0.55
6.5	8.44	8.26	7.19	6.52	6.48	5.70	5.38	4.54	3.92	3.60	2.62	2.29	2.25	1.28	1.00	0.64
7	8.17	8.19	7.26	6.49	6.21	5.45	4.78	5.04	3.85	3.40	2.65	2.24	1.81	1.21	0.99	1.11
7.5	8.08	8.13	6.98	6.18	5.90	5.31	4.65	4.37	3.67	3.69	2.65	2.28	1.56	1.32	0.93	0.44
8	7.87	7.92	7.04	6.41	5.86	4.91	4.87	4.76	3.68	3.28	2.73	2.15	1.47	1.00	0.75	0.27
8.5	7.75	7.69	6.81	6.18	5.62	5.01	4.93	4.62	3.46	2.86	2.97	1.84		1.02	0.73	0.29
9	7.62	7.47	6.78	5.85	5.63	4.94	4.79	4.58	3.35	2.90	2.52	1.81		1.03	0.30	0.27
9.5	7.45	7.33	6.71	5.63	5.64	5.21	4.78	4.47	3.12	2.93	2.43	1.31		0.76	0.21	0.25
10	7.27	7.19	6.52	4.88	5.60	5.20	4.19	3.62	3.21	2.66	2.35			0.48	0.19	0.25
10.5	7.16	7.11	6.22	4.46	5.53	4.97	3.90	3.72	3.11	2.39	1.58			0.32		0.24
11	7.04	7.03	6.00		5.40	4.81	3.65	3.09		1.58	1.05			0.16		
11.5	6.83	6.81			3.20	4.64	3.31	2.52		0.76	0.54			0.16		
12	6.61	6.69				4.27		2.20						0.15		
12.5	6.52					4.01										
13	6.42					3.69										

Depth	02-Oct	11-Oct	17-Oct	24-Oct	31-Oct	07-Nov	14-Nov	11-Dec	18-Dec	09-Jan	15-Jan	21-Jan	29-Jan	05-Feb	26-Feb	13-Mar	19-Mar
0	9.39	10.33	10.90	11.55	14.57	12.54	12.50	ice	ice	ice	ice	ice	ice	ice	ice	ice	ice
0.5	9.36	10.33	10.82	11.52	9.44	12.54	12.36	10.94	11.76	10.15	10.12	ice	ice	ice	ice	ice	ice
1	9.33	10.27	10.78	11.46	9.40	12.52	12.34	9.93	10.76	9.89	8.93	9.50	9.24	8.76	7.59	7.42	7.75
1.5	9.31	10.24	10.76	11.45	9.38	12.52	12.29	9.79	10.43	9.69	8.69						
2	9.28	10.22	10.74	11.46	9.36	12.50	12.29	9.75	10.30	9.55	8.66	9.10	8.48	8.41	6.75	6.93	6.74
2.5	9.14	10.22	10.74	11.47	9.37	12.50	12.28	9.70	10.26	9.35	8.65						
3	9.13	10.21	10.72	11.51	9.34	12.50	12.26	9.63	10.22	9.04	8.51	9.00	8.21	8.30	7.06	6.79	6.55
3.5	8.93	10.20	10.70	11.49	9.34	12.49	12.26	9.56	10.06	8.79	8.36						
4	7.61	10.15	10.68	11.49	9.34	12.47	12.25	9.50	10.03	8.54	8.17	8.68	8.01	7.86	6.15	6.60	6.38
4.5	2.76	10.11	10.66	11.49	9.34	12.47	12.26	9.43	9.89	8.35	7.97						
5	0.33	10.05	10.62	11.49	9.33	12.47	12.25	9.36	9.78	8.26	7.67	8.03	7.54	7.21	6.63	6.26	5.99
5.5	0.31	9.90	10.58	11.49	9.32	12.47	12.25	9.31	9.65	8.02	7.56						
6	0.30	0.38	10.57	11.34	9.32	12.46	12.25	9.28	9.58	7.89	7.45	7.68	7.22	6.96	5.91	5.55	5.49
6.5	0.34	0.34	10.51	11.37	9.32	12.46	12.22	9.19	9.41	7.81	7.38						
7	0.32	0.33	10.27	11.38	9.31	12.45	12.22	8.94	9.23	7.64	7.27	7.48	6.78	6.69	5.29	4.91	5.01
7.5	0.29	0.32	5.10	11.32	9.32	12.44	12.22	8.74	8.99	7.50	7.09						
8	0.28	0.30	0.34	11.29	9.31	12.43	12.22	8.61	8.88	7.43	6.99	7.14	6.42	6.12	4.63	4.88	4.29
8.5		0.31	0.29	10.48	9.31	12.43	12.22	8.54	8.73	7.26	6.84						
9		0.31	0.28	4.56	9.31		12.22	8.36	8.69	7.02	6.62	6.59	5.71	5.69	4.00	4.31	3.98
9.5		0.30	0.28	3.11			12.22	8.28	8.60	6.68	6.25						
10		0.31	0.25	2.60			12.22	8.17	8.47	6.52	5.94	5.92	5.32	5.24	4.28	4.11	3.61
10.5		0.30		0.55			12.22	8.11	8.40	6.24	5.62						
11		0.29					12.22	7.95	8.16	5.58	5.38	5.34	4.91	4.57	3.20	3.16	3.10
11.5							12.22	7.79	7.80	5.33	5.04						
12							12.22	7.47	7.39	5.15	4.69	4.94	4.21	3.82		1.61	1.69
12.5							12.22	7.07	6.87	4.75	3.28						
13							12.22	6.80	6.68	4.19	3.10	4.13	4.15	2.35			0.77
13.5							12.22	6.36	6.07	3.94	3.20						

Table A3- 7. Profiles of light attenuation in Lac Croche, measured as the ratio of light at depth, I, to light available at the surface, I_0. Light extinction coefficients (ε_{par}, m^{-1}) were calculated from the slope of the line of the natural log of I/I_0 with depth.

Depth	May-23	Jun-03	Jun-20	Jul-01	Jul-15	Jul-29	Aug-11	Aug-23	Sep-03	Sep-17	Oct-01	Oct-23	06-Nov
0	0.8291	0.8968	0.8756	0.8421	0.8022	0.6982	0.8431	0.7041	0.7041	0.7445	0.7525	0.6096	0.9859
0.5	0.4891	0.6543	0.5323	0.6008	0.5015	0.5387	0.5256	0.4913	0.5067	0.5098	0.5100	0.3943	0.6493
1	0.3098	0.3977	0.3858	0.4572	0.3252	0.4084	0.4835	0.3401	0.3663	0.3678	0.3614	0.2588	0.4395
1.5	0.2080	0.2998	0.2563	0.0322	0.1928	0.2986	0.2902	0.2558	0.2599	0.2628	0.2467	0.1849	0.3083
2	0.1998	0.1754	0.1821	0.2430	0.1724	0.2359	0.2479	0.1688	0.1844	0.1788	0.1727	0.1047	0.1911
2.5	0.1292	0.1530	0.1019	0.1780	0.1228	0.1488	0.1807	0.1317	0.1477	0.1322	0.1377	0.0954	0.1643
3	0.0971	0.1139	0.0843	0.1225	0.0875	0.1012	0.1264	0.1050	0.1013	0.1049	0.0868	0.0673	0.1107
3.5	0.0692	0.0815	0.0551	0.0950	0.0564	0.0849	0.1005	0.0797	0.0746	0.0791	0.0733	0.0477	0.0843
4	0.0449	0.0659	0.0446	0.0731	0.0447	0.0662	0.0742	0.0543	0.0603	0.0605	0.0583	0.0341	0.0632
4.5	0.0388	0.0444	0.0296	0.0557	0.0312	0.0459	0.0587	0.0423	0.0445	0.0445	0.0404	0.0233	0.0435
5	0.0274	0.0310	0.0229	0.0366	0.0249	0.0277	0.0405	0.0333	0.0324	0.0324	0.0349	0.0165	0.0340
5.5	0.0191	0.0256	0.0171	0.0310	0.0162	0.0223	0.0275	0.0205	0.0260	0.0260	0.2579	0.0126	0.1415
6	0.0132	0.0184	0.0126	0.0233	0.0126	0.0068	0.0206	0.0143	0.0178	0.0178	0.1832	0.0091	0.1007
6.5	0.0109	0.0126	0.0000	0.0153	0.0077	0.0000	0.0134	0.0095	0.0131	0.0131	0.0000	0.0000	0.0000
7	0.0000	0.0000	0.0000	0.0120	0.0000	0.0000	0.0000	0.0000	0.0092	0.0092	0.0000	0.0000	0.0000
7.5	0.0000	0.0000	0.0000	0.0059	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
ε_{par}	0.58	0.64	0.70	0.60	0.68	0.69	0.61	0.62	0.6	0.59	0.60	0.69	0.68

Table A3- 8. Profiles of light attenuation in Lac à l'Ours, measured as the ratio of light at depth to light available at the surface. Light extinction coefficients (ε_{par}, m^{-1}) were calculated from the slope of the line of the natural log of I/I_0 with depth.

Depth	22-May	04-Jun	21-Jun	03-Jul	17-Jul	31-Jul	13-Aug	24-Aug	04-Sep	12-Sep	18-Sep	02-Oct	24-Oct	31-Oct	13-Nov
0	0.7566	0.7310	0.8029	0.7460	0.7712	0.7868	0.8260	0.8651	0.5379	0.6054	0.6729	0.7730	0.7163	0.6595	0.6595
0.5	0.3214	0.2499	0.4144	0.3317	0.3434	0.4049	0.4151	0.4252	0.2318	0.2452	0.2585	0.2805	0.2704	0.2602	0.2602
1	0.1488	0.1468	0.2127	0.1536	0.1760	0.2126	0.2284	0.2441	0.1343	0.1508	0.1673	0.2204	0.1691	0.1178	0.1178
1.5	0.0279	0.0933	0.1238	0.0745	0.0925	0.1069	0.1120	0.1171	0.0812	0.0847	0.0882	0.1867	0.1199	0.0530	0.0530
2	0.0103	0.0439	0.0684	0.0371	0.0512	0.0466	0.0544	0.0622	0.0369	0.0449	0.0529	0.0582	0.0415	0.0249	0.0249
2.5	0.0049	0.0214	0.0536	0.0157	0.0276	0.0324	0.0324	0.0323	0.0191	0.0232	0.0273	0.0298	0.0216	0.0134	0.0134
3	0.0000	0.0140	0.0446	0.0076	0.0144	0.0102	0.0135	0.0168	0.0111	0.0128	0.0145	0.0156	0.0115	0.0074	0.0074
3.5	0.0000	0.0079	0.0362	0.0000	0.0076	0.0075	0.0081	0.0087	0.0051	0.0070	0.0089	0.0100	0.0050	0.0000	0.0000
4	0.0000	0.0000	0.0285	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
ε_{par}	2.12	1.25	1.11	1.52	1.30	1.37	1.33	1.31	1.30	1.21	1.24	1.50	1.38	1.50	1.50

Appendix 4 Bottle incubation data from twenty-one lakes sampled in 2003

Table A4- 9. Bottle incubation measurements made to calculate respiration in the lakes sampled in 2003. Temperature is shown in °C, length of incubations in h., oxygen concentrations are in mg L^{-1} and respiration in mg O_2 m^{-3} h^{-1}. Confidence intervals of respiration are shown as ± one standard error (SE) of *n* replicates.

Achigan

Date	22-May		17-Jun		30-Jun		30-Jul		11-Sep		29-Oct	
Temperature		14		17		24		21		19		8
Length		6		8.13		6.33		6.17		6.1		6.36
	initial	black	initial	black	initial	black	initial	black	initial	black	initial	black
Replicate [O_2]	9.8182	9.7543	8.4956	8.4391	7.9823	7.8797		8.1694	8.4879	8.4701	10.5449	10.512
	9.8211	9.7767	8.5096	8.4269	7.9866	7.9317	8.2214	8.1812	8.4834	8.4576	10.5613	10.5235
	9.8179	9.7711	8.5022	8.4205		7.8908	8.2183	8.192	8.4810	8.4749	10.5515	10.5419
	9.8253	9.7846	8.5215	8.4559	7.9745	7.93001	8.1928	8.1766	8.4864		10.5444	
Average [O_2]	9.8206	9.7717	8.5072	8.4356	7.9811	7.9081	8.2108	8.1798	8.4847	8.4675	10.5505	10.5258
R	8.16±1.11		8.81±1.18		11.55±1.17		5.03±1.49		2.81±0.89		3.89±1.54	

Blanche

Date	15-May		17-Jun		03-Aug		09-Sep		29-Oct			
Temperature		9		16		21		18		7		
Length		7.08		7.92		7.83		6.42		6.17		
	initial	black	initial	black	initial	black	initial	black	initial	black	initial	black
Replicate [O_2]	9.6469	9.6463	9.2488	9.1612		7.986	8.8061	8.7843	11.1590	11.1295		
	9.6525	9.6453	9.2332	9.1643	8.0201	7.9586	8.8045	8.7752	11.1746	11.135		
	9.6454	9.6429	9.2318	9.1488	8.0052	7.9793	8.8031	8.7715	11.1586			
	9.6524	9.6546	9.2401		8.0155	7.9677	8.8021		11.1794			
Average [O_2]	9.6493	9.6473	9.2385	9.1581	8.0136	7.9729	8.8040	8.7770	11.1679	11.1323		
R	0.29±0.44		10.15±0.82		5.20±0.92		4.20±0.61		5.78±1.30			

Connelly

Date	21-May		17-Jun		30-Jun		30-Jul		11-Sep	
Temperature		16		19.6		24		21		18
Length		8.17		7.75		6.17		6		6
	initial	black	initial	black	initial	black	initial	black	initial	black
Replicate [O_2]	9.2243	9.1616	8.4923	8.4099	7.9431	7.84378		8.2497	8.6585	8.594
	9.2288	9.1715	8.5040	8.4134	7.9321		8.2947	8.245	8.6533	8.5991
	9.2199	9.1462	8.4960			7.84	8.2982	8.2608	8.6631	
	9.2222					7.82237	8.3080	8.256		
Average [O_2]	9.2238	9.1598	8.4974	8.4117	7.9376	7.8354	8.3003	8.2529	8.6583	8.5966
R	7.84±0.94		11.07±0.59		16.57±0.29		7.90±0.82		10.29±0.72	

En Coeur

Date	13-May		12-Jun		04-Jul		02-Aug		11-Sep	
Temperature		10		17		23		22		18
Length		7.17		6		5.9		7.17		5.93
	initial	black	initial	black	initial	black	initial	black	initial	black
Replicate [O_2]		10.0666	9.0689		8.0521	7.9672	8.3545	8.2687	8.7215	8.6035
		10.0604	9.0680	9.0387	8.0547		8.3601	8.2678	8.6516	8.6027
	10.0634	10.0583	9.0624	9.0493	8.0571	7.9661	8.3547	8.2904	8.6558	8.606
	10.0666			9.0162	8.0645	7.9641	8.3539	8.2881		
Average [O_2]	10.0650	10.0617	9.0664	9.0347	8.0571	7.9658	8.3558	8.2788	8.6763	8.6041
R	0.45±0.39		5.28±1.66		15.47±0.54		10.75±0.87		12.18±3.82	

Gervais

Date	13-May		10-Jun		02-Jul		29-Jul		09-Sep		28-Oct	
Temperature		10		18		22		21		19		8
Length		8		7.08		5.25		7.17		6.28		7.23
	initial	black	initial	black	initial	black	initial	black	initial	black	initial	black
Replicate [O_2]	10.1800	10.0801	8.7562	8.6574	8.0806	8.0412		7.9607	8.3184	8.2949	10.9388	10.9056

	10.1512	10.0856	8.7386	8.6883	8.0932	7.9407	7.9953	7.9447	8.3286	8.3162	10.9313	10.9148
	10.1883		8.7513	8.6883	8.0855	8.0521	8.0134	7.9734	8.3221	8.3157	10.9380	10.9282
	10.1652	10.0798		8.664	8.0859	7.9948	7.9952	7.9567	8.3243		10.9325	
Average [O_2]	10.1712	10.0818	8.7487	8.6745	8.0863	8.0072	8.0013	7.9589	8.3234	8.3089	10.9352	10.9162
R	11.17±1.21		10.48±1.31		15.07±4.87		5.91±1.10		2.30±1.18		2.62±0.96	

Montange Noire

Date	19-May		17-Jun		07-Jul		29-Jul		09-Sep		27-Oct	
Temperature		10		15		23		22		18		7
Length		7.62		5.67		8.07		7.33		6.33		6.33
	initial	black	initial	black	initial	black	initial	black	initial	black	initial	black
	9.3259	9.2959	9.3632	9.2679	7.8248	7.7747	8.5454	8.5072	8.9790	8.9615	11.4257	11.3954
Replicate [O_2]	9.3251	9.2869	9.3299	9.2482	7.8259	7.7752	8.5475	8.5031	8.9979	8.9451	11.4342	11.425
	9.3259	9.2810	9.3451		7.8295	7.767		8.506	8.9858	8.9421	11.4176	11.4064
	9.3108	9.2904	9.3385		7.8246	7.7806		8.5052			11.4237	
Average [O_2]	9.3219	9.2886	9.3442	9.2581	7.8262	7.7744	8.5465	8.5054	8.9876	8.9496	11.4253	11.4089
R	4.38±0.64		15.19±2.47		6.42±0.37		5.60±0.16		6.00±1.29		2.59±1.50	

du Nord

Date	20-May		18-Jun		04-Jul		29-Jul		11-Sep		29-Oct	
Temperature		16		20		23		23		19		8
Length		7		4.82		6.08		9		6.3		6.48
	initial	black	initial	black	initial	black	initial	black	initial	black	initial	black
	9.1100	9.0397			8.1070	8.0368	8.3342	8.2216	8.3481	8.2774	11.2978	11.2903
Replicate [O_2]	9.1275	9.0397	8.4314	8.3674	8.0998	8.0529	8.3306	8.2313	8.3378		11.3054	11.2969
	9.1160		8.4360	8.344	8.1152	8.041	8.3410	8.2376	8.3403	8.2622	11.3169	11.3171
	9.1119	9.0355	8.4489	8.323	8.0976	8.0227	8.3499	8.2149	8.3413	8.2026	11.3169	11.2878
Average [O_2]	9.1164	9.0383	8.4388	8.3448	8.1049	8.0384	8.3389	8.2264	8.3419	8.2474	11.3093	11.2980
R	11.15±0.68		19.49±2.88		10.95±1.22		12.51±0.73		15.00±3.65		1.73±1.25	

Ouimet

Date	16-May		10-Jun		02-Jul		29-Jul		12-Sep		28-Oct	
Temperature		12		18		22		21		19		8
Length		6		7		7.17		7.16		6.08		7
	initial	black	initial	black	initial	black	initial	black	initial	black	initial	black
Replicate [O_2]		9.8155	8.8339	8.7476	7.9986	7.9404	8.2694	8.2131	8.2990	8.2492	10.8949	10.8664
	9.8631	9.8204	8.8165		7.9920	7.912	8.2518	8.2143	8.3086	8.259	10.8985	10.8619
	9.8685	9.8133	8.8332	8.7446	8.0064	7.9075	8.2664		8.2984	8.2504	10.8919	10.8584
	9.8424	9.8199	8.8309		7.9999	7.9368	8.2650	8.2272	8.3001		10.8970	
Average [O_2]	9.8580	9.8173	8.8286	8.7461	7.9992	7.9242	8.2632	8.2182	8.3015	8.2529	10.8956	10.8622
R	6.79±1.18		11.79±0.85		10.47±1.24		6.28±0.89		8.00±0.68		4.76±0.41	

Pin Rouge

Date	13-May		17-Jun		07-Jul		31-Jul		08-Sep		27-Oct	
Temperature		20		19.6		23		23		18		7
Length		6.83		5.75		7.93		8.13		6.12		5.83
	initial	black	initial	black	initial	black	initial	black	initial	black	initial	black
Replicate [O_2]	8.7900	8.6555	8.4210	8.3222	7.5066	7.4193	8.2608	8.1616	8.5954	8.4784	10.4160	10.3981
	8.7181	8.6458	8.4064		7.5131	7.4095	8.2600	8.1575	8.5456	8.4736	10.4130	10.3627
		8.6250	8.4144	8.3199	7.5088	7.4177	8.2686	8.1664	8.5426	8.4701	10.4070	10.3733
	8.7404	8.6469	8.4199	8.3186	7.5088		8.2592		8.5486	8.4736		
Average [O_2]	8.7495	8.6433	8.4154	8.3202	7.5093	7.4155	8.2622	8.1618	8.5581	8.4739	10.4120	10.3780
R	15.55±2.86		16.56±0.69		11.83±0.43		12.34±0.44		13.75±2.06		5.83±1.86	

Rouge

Date	15-May		11-Jun		01-Jul		29-Jul		09-Sep		27-Oct	
Temperature		9		16		22		22		18		7
Length		6.67		6.12	Length:	8.08		5.75		6.33		6
	initial	black	initial	black	initial	black	initial	black	initial	black	initial	black
Replicate [O_2]	10.1236	10.089	9.2571	9.2437	8.1698	8.0999	8.2008	8.1782	8.7067	8.6615	10.7422	10.7322

	10.1327	10.109	9.2472	9.1949	8.1767	8.095	8.2051	8.1691	8.6995	8.6823	10.752	10.7254
	10.1121	10.107	9.2437	9.2157	8.1682	8.0877	8.2055	8.1673	8.7096	8.6538	10.7575	10.7247
			9.2451	9.1727	8.1589	8.0756		8.1648	8.7127		10.7481	
Average [O_2]	10.1228	10.1017	9.2483	9.2068	8.1684	8.0896	8.2038	8.1699	8.7071	8.6659	10.7500	10.7274
R	3.17±1.33		6.79±2.52		9.76±0.80		5.90±0.56		6.52±1.44		3.75±0.74	

des Sables

Date	14-May		09-Jun		03-Jul		29-Jul		10-Sep		26-Oct	
Temperature		10		17		23		22		18		7
Length		7.5		7.7		6		7.75		6.55		6.02
	initial	black	initial	black	initial	black	initial	black	initial	black	initial	black
	9.8645		9.0160	8.9691	7.7651	7.6756	8.2020		8.7272	8.6633	11.3555	11.3371
Replicate [O_2]	9.85266	9.8199	9.0261	8.9709	7.7676	7.6975	8.1927	8.1465	8.7186	8.678	11.3402	11.3061
	9.85545	9.8369	9.0150	8.9676	7.7708	7.7208	8.1896	8.1366	8.7328	8.673	11.3428	11.3237
	9.85934	9.8144	9.0070	8.9589	7.7675	7.7048	8.2038	8.1387	8.7199		11.3523	
Average [O_2]	9.8580	9.8237	9.0160	8.9666	7.7678	7.6997	8.1970	8.1406	8.7246	8.6714	11.3477	11.3223
R	4.57±0.99		6.42±0.61		11.35±1.58		7.28±0.65		8.12±0.88		4.22±1.65	

St.Joseph

Date	22-May		18-Jun		03-Jul		04-Aug		10-Sep		26-Oct	
Temperature		14		18		23		22		18		7
Length		6.38		6		5.83		7.67		6.47		6
	initial	black	initial	black	initial	black	initial	black	initial	black	initial	black
	9.4271	9.3925	8.1465		8.0146		8.1071	8.0326	8.7826	8.7074	11.1296	
Replicate [O_2]	9.4173	9.3801	8.1530	8.095	8.0023	7.9584	8.1096	8.0431	8.7871	8.728	11.1215	11.1228
	9.4302		8.1454	8.0882	7.9987	7.952	8.1094	8.0529	8.7869	8.7126	11.1192	11.1092
			8.1507	8.0804	8.0081	7.9458	8.1121		8.7745			
Average [O_2]	9.4249	9.3863	8.1489	8.0879	8.0059	7.9521	8.1096	8.0429	8.7828	8.7160	11.1234	11.1160
R	6.04±1.23		10.17±0.78		9.24±0.93		8.69±0.78		10.32±1.09		1.24±1.30	

Tremblant

Date	12-May		12-Jun		02-Jul		05-Aug		12-Sep		28-Oct	
Temperature		6		14		20		22		19		8
Length		6		7		8.25		5.92		6.23		7.13
	initial	black	initial	black	initial	black	initial	black	initial	black	initial	black
Replicate [O_2]	10.9907	10.9809	9.2345		8.0218	7.9896	7.9767	7.9557	8.3639	8.3693	10.7179	10.6994
	10.9864	10.9734	9.2246	9.2177	8.0273	7.9924	7.9732	7.9668	8.3771	8.3528	10.7162	10.7122
		10.9809	9.2096	9.2026	8.0420	7.9983	7.9695	7.9797	8.3716	8.3353	10.7294	10.6852
	10.9770		9.2236	9.2174	8.0465	7.9989	7.9858	7.9536				
Average [O_2]	10.9847	10.9784	9.2231	9.2126	8.0344	7.9948	7.9763	7.9640	8.3709	8.3525	10.7212	10.6989
R	1.05±0.79		1.50±1.10		4.80±0.76		2.09±1.17		2.95±1.69		3.12±1.24	

à la Truite

Date	14-May		09-Jun		03-Jul		03-Aug		10-Sep		26-Oct	
Temperature		10		17		22		21		18		7
Length		7.27		7.67		6.25		7.63		6.58		6.25
	initial	black	initial	black	initial	black	initial	black	initial	black	initial	black
Replicate [O_2]	10.4146	10.3735	9.1233	9.0999	7.8532	7.8107	8.1329		8.8199	8.7949	11.2720	11.2565
	10.4052	10.3754	9.1282	9.0764		7.8349	8.1304		8.8109	8.7894	11.2786	11.2355
	10.4037	10.3545	9.1214	9.0891	7.8517	7.7989	8.1347	8.0646	8.8097	8.7754		11.2062
	10.4189	10.3653	9.1219	9.0787	7.8282		8.1362	8.0653				
Average [O_2]	10.4106	10.3672	9.1237	9.0860	7.8444	7.8148	8.1336	8.0650	8.8135	8.7866	11.2753	11.2327
R	5.97±0.83		4.91±0.73		4.73±2.13		8.99±0.24		4.09±1.01		6.81±2.37	

Argent

Date	27-May		22-Jul		02-Nov	
Temperature		18		21		7
Length		7		6.08		6.5
	initial	black	initial	black	initial	black
Replicate [O_2]	9.3981	9.3454	8.1555	8.08	10.5269	10.5265

	9.3946	9.3563	8.1706	8.086	10.5221	10.5065
	9.3963	9.3419	8.1595	8.0979	10.5142	10.4803
	9.3951	9.3594	8.1697			
Average [O_2]	9.3960	9.3508	8.1638	8.0880	10.5211	10.5044
R	6.47±0.61		12.48±1.12		2.56±2.14	

Bowker						
Date	27-May		22-Jul		02-Nov	
Temperature		12.4		21		7
Length		6.17		6.08		6
	initial	black	initial	black	initial	black
		10.5497	8.6436		10.6843	10.6761
Replicate [O_2]	10.5553	10.5447	8.6425	8.6161	10.6986	10.6583
	10.5607	10.5384	8.6478	8.6025	10.6892	
	10.5693	10.5418	8.6332	8.6129		
Average [O_2]	10.5618	10.5437	8.6418	8.6105	10.6907	10.6672
R	2.94±0.69		5.14±0.89		3.92±1.71	

Brome						
Date	28-May		23-Jul		03-Nov	
Temperature		16		22		7.4
Length		6.27		6.8		6
	initial	black	initial	black	initial	black
	10.1253	9.9388	8.2209	8.124	10.7534	
Replicate [O_2]	10.1091		8.2360		10.7478	10.7079
	10.1192		8.2378	8.124	10.7512	10.694
	10.1188		8.2312		10.7432	
Average [O_2]	10.1181	9.9388	8.2315	8.1240	10.7489	10.7010
R	28.60		15.81±0.79		7.99±1.27	

Orford

Date	27-May		22-Jul		02-Nov	
Temperature		13.7		21		7
Length		6.08		6		7.75
	initial	black	initial	black	initial	black
Replicate [O_2]	10.1324	10.0716	8.6843	8.6056	10.7937	10.7347
	10.1253	10.0945	8.6445	8.6229		10.7484
	10.1329	10.0880	8.6730	8.6191	10.7967	
	10.1093	10.0834			10.7916	
Average [O_2]	10.1250	10.0844	8.6673	8.6159	10.7940	10.7416
R	6.68±1.20		8.57±2.16		6.77±0.91	

Waterloo

Date	28-May		23-Jul		03-Nov	
Temperature		16		22		7.4
Length		7.15		6.17		7.4
	initial	black	initial	black	initial	black
Replicate [O_2]	9.5423	9.4086	7.9229	7.7088	9.9779	9.9252
		9.3976	7.9167	7.6926	9.9751	9.908
	9.5332	9.4034	7.9138	7.6983	9.9477	9.9157
	9.5582	9.4045		7.6807		
Average [O_2]	9.5446	9.4035	7.9178	7.6951	9.9669	9.9163
R	19.73±0.94		36.09±1.02		6.84±1.47	

La Peche

Date	03-Jun		25-Jul		31-Oct	
Temperature		15.6		21		9
Length		6.33		6		5.83
	initial	black	initial	black	initial	black
Replicate [O_2]	9.7366	9.6366	8.6567	8.5433	10.0631	10.0433

		9.6538	8.6592	8.5601	10.0790	10.0468
		9.6477	8.6499	8.5605	10.0638	10.0366
	9.7357		8.6574	8.5532		10.0203
Average [O_2]	9.7362	9.6460	8.6558	8.5543	10.0686	10.0368
R	14.24±0.80		16.92±0.75		5.46±1.27	

Phillippe

Date	03-Jun		25-Jul		31-Oct	
Temperature		17.4		21.6		9
Length		7.75		6.16		5.83
	initial	black	initial	black	initial	black
	9.7770	9.6606	8.5646	8.4958	10.2481	10.2373
Replicate [O_2]	9.7518	9.6702	8.5538	8.5056		10.2429
	9.7658		8.5599		10.2487	10.2132
	9.7645		8.5523		10.2639	
Average [O_2]	9.7648	9.6654	8.5577	8.5007	10.2536	10.2311
R	12.82±1.13		9.25±1.03		3.85±1.80	

Appendix 5 Carbon dioxide profiles in lakes Croche and à l'Ours

Table A5- 10. Carbon dioxide profiles in Lac Croche (µmol L^{-1}) between June 2002 and January 2003.

Depth	20-Jun	26-Jun	1-Jul	8-Jul	15-Jul	23-Jul	29-Jul	7-Aug	11-Aug	23-Aug	29-Aug	3-Sep	11-Sep	15-Sep	27-Sep
0.0	35.5	26.2	22.9	19.7	15.3	23.7	29.2	22.6	23.8	23.2	25.2	23.6	22.1	28.3	27.5
1.0	34.0	25.1	26.8	19.8	17.2	21.0	24.0	26.6	24.9	26.2	26.4	25.5	22.7	29.4	27.9
2.0	32.4	28.3	21.2	19.3	17.5	19.9	23.9	22.9	24.6	32.1	26.4	26.3	24.1	28.4	29.3
3.0	35.1	28.9	25.5	22.7	17.9	22.6	27.4	30.9	23.9	27.0	24.8	26.9	31.6	29.6	31.3
4.0	38.1	41.2	37.8	42.0	39.8	44.9	65.0	28.0	36.6	25.4	30.1	27.0	27.2	28.8	25.8
5.0	48.3	46.2	47.5	61.2	53.0	49.2	97.5	48.6	55.2	60.5	63.1	43.2	141.8	30.5	30.1
6.0	65.9	59.5	74.1	132.4	92.6	118.1	129.3	69.0	50.2	113.8	119.8	341.8	322.7	170.3	178.7
7.0	216.1	109.2	100.6	234.1	198.3	206.9	237.2	254.0	319.9	278.5	317.2	49.0	268.6	318.5	341.7
8.0	214.6	149.5	170.3	206.4	344.3	295.8	362.7	333.8	343.5	363.2	357.7			355.0	372.0
9.0	220.3	212.3	174.1												

Depth	1-Oct	9-Oct	16-Oct	23-Oct	30-Oct	6-Nov	13-Nov	4-Dec	18-Dec	9-Jan	15-Jan	21-Jan	29-Jan
0.0	39.8	56.8	67.2	65.2	65.5	65.3	60.5	52.6	41.6	73.3	84.5	106.4	112.9
1.0	42.6	58.4	64.1	61.0	64.4	59.8	60.5	52.6	51.6	73.3	84.5	106.4	112.9
2.0	42.6	56.3	63.1	63.6	62.6	60.6	61.0	52.6	61.6	73.3	84.5	106.4	112.9
3.0	43.8	56.1	60.4	64.3	58.6	59.1	60.3	52.6	71.6	73.3	84.5	106.4	112.9
4.0	43.7	56.0	63.6	59.6	62.8	60.0	60.5	52.6	81.6	73.3	84.5	106.4	112.9
5.0	45.7	56.3	63.6	63.0	63.4	58.8	57.9	52.6	91.5	73.3	84.5	106.4	112.9
6.0	132.9	57.5	61.6	64.0	65.6	61.1	59.8	52.6	101.5	73.3	84.5	106.4	112.9
7.0	256.9	137.4	65.4	65.2	66.1	62.7	59.8	82.3	111.5	113.9	168.5	215.2	170.4
8.0	356.5	351.2	191.9	61.4	65.2	61.1	62.3	89.7	121.5	124.1	189.5	242.4	184.8
9.0					63.8			7.4	10.0	10.2	21.0	27.2	14.4

Table A5- 11. Carbon dioxide profiles in Lac à l'Ours (μmol L^{-1}) between June 2002 and January 2003.

Depth	21-Jun	27-Jun	3-Jul	10-Jul	17-Jul	24-Jul	31-Jul	8-Aug	13-Aug	24-Aug	30-Aug	4-Sep	18-Sep	26-Sep
0.0	51.0	35.7	30.1	26.5	26.5	34.3	29.8	34.8	22.7	30.9	29.5	27.6	55.3	47.8
1.0	47.0	35.8	29.5	26.5	27.5	28.7	35.7	33.5	25.6	32.3	28.7	30.2	55.6	42.5
2.0	55.3	33.6	34.5	26.7	29.7	24.4	28.2	32.2	23.8	34.2	31.5	31.0	55.8	47.1
3.0	69.1	43.3	50.8	68.7	58.8	56.4	116.3	60.9	51.6	47.5	30.0	42.3	55.9	40.9
4.0	88.5	118.2	170.6	177.6	170.0	158.8	168.7	191.2	243.6	211.3	185.8	200.6	101.4	106.9
5.0	86.1	154.3	206.6	223.5	227.5	235.1	340.5	257.5	286.1	293.4	287.5	376.9	393.0	345.8
6.0	164.3	180.9	213.1	233.0	226.6	273.2	327.3	261.8	275.3	286.4	289.7	349.8	362.6	319.1
7.0	175.1	190.5	217.2	248.5	245.9	280.5	330.6	251.3	286.9	277.6	254.3	323.2	370.7	319.1
8.0	182.0	188.1	246.1	263.9	248.5	271.4	354.6	240.7	300.2	312.8	304.9	322.3	389.1	330.7
9.0	189.5	208.5	254.8	263.2	253.0	293.1	363.3	273.6	308.8	283.8			397.2	357.4
10.0	199.9	209.7	251.8	272.8	253.0	295.5	386.5	281.4	319.3					345.2
11.0	210.2	229.9	249.5	293.7	275.1				349.5					

Depth	2-Oct	10-Oct	17-Oct	24-Oct	31-Oct	7-Nov	14-Nov	4-Dec	11-Dec	18-Dec	9-Jan	15-Jan	21-Jan	29-Jan
0.0	337.0	85.1	89.2	93.2	115.2	106.0	120.2	91.1	136.7	108.2	165.2	203.9	172.9	138.3
1.0	51.7	80.4	87.3	94.3	122.6	106.0	114.3	91.1	139.8	110.9	165.2	200.3	172.9	138.3
2.0	57.1	85.6	87.1	98.2	125.5	106.0	119.3	91.1	142.9	113.6	165.2	196.7	172.9	138.3
3.0	56.0	82.7	86.9	96.8	129.1	106.0	110.2	91.1	146.0	116.3	165.2	193.1	172.9	138.3
4.0	57.9	86.1	92.5	98.9	125.8	106.0	116.7	91.1	149.1	116.3	165.2	193.1	172.9	138.3
5.0	234.8	80.2	91.4	102.5	124.2	106.0	115.9	91.1	152.2	116.3	165.2	193.1	172.9	138.3
6.0	300.6	88.3	98.6	108.8	127.2	106.0	115.6	91.1	155.3	124.4	165.2	193.1	172.9	138.3
7.0	311.4	279.4	165.8	146.0	126.2	106.0	119.1	91.1	161.5	128.6	165.2	193.1	172.9	138.3
8.0		327.5	279.9	200.6	121.4	106.0	116.4	91.1	167.8	132.9	165.2	193.1	172.9	138.3
9.0		333.2	320.6	160.3		106.0	115.9	91.1	174.0	137.1	136.1	193.1	172.9	138.3
10.0				236.3		106.0	116.1	125.4	174.7	138.4	136.1	193.1	172.9	207.2
11.0						106.0	115.8	125.4	175.3	139.8	136.1	286.7	308.3	207.2
12.0						106.0	116.5	125.4	174.7	141.1	136.1	298.4	308.3	207.2

Appendix 6 Carbon isotopes and fluxes from lakes sampled in 2003.

Table A6- 12. Temperature (T, °C), pH, dissolved inorganic carbon (DIC, g m^{-3}), carbon dioxide saturation (CO_{2sat}), CO_2 flux to the atmosphere (CO_2 flux, mg C m^{-2} d^{-1}), isotopic composition of dissolved inorganic carbon, dissolved CO_2, and dissolved organic carbon ($\delta^{13}C_{DIC}$, $\delta^{13}C_{CO2}$, $\delta^{13}C_{DOC}$, ‰ VPDB).

Lake	Date	T	pH	[DIC]	CO_{2sat}	CO_2 flux	$\delta^{13}C_{DIC}$	$\delta^{13}C_{CO2}$	$\delta^{13}C_{DOC}$
Achigan	22-May	13.7	6.53	1.74	1.57	60	-7.4	-14.8	-28.1
	16-Jun	17.5	6.45	3.00	1.64	187	-7.2	-14.3	-28.5
	30-Jun	23.5	6.84	2.39	3.53	300	-8.6	-14.4	-27.9
	30-Jul	21.0	7.40	1.06	4.27	109	0.3	-5.1	-27.5
	11-Sep	19.0	7.52	2.00	1.33	54	-4.1	-11.4	-27.5
	29-Oct	7.0	6.04	0.76	1.86	-26	-5.4	-12.6	-27.3
Blanche	15-May	9.3	5.97	0.60	2.36	60	-15.7	-18.8	-27.7
	11-Jun	16.2	6.90	0.70	0.74	-15	-17.8	-24.4	-27.9
	1-Jul	22.0	6.87	0.53	1.07	169	-9.3	-14.6	-27.4
	2-Aug	21.2	7.01	0.31	1.50	-40	-12.0	-17.3	-26.7
	9-Sep	18.0	6.97	0.61	2.92	199	-5.7	-10.0	-27.4
	27-Oct	7.7	6.01	0.44	3.49	10	-12.9	-15.1	-27.0
Connely	20-May	16.2	6.92	3.38	1.22	23	-5.2	-13.2	-27.7
	16-Jun	16.3	7.50	5.41	0.97	214	-6.7	-14.5	-27.1
	30-Jun	24.7	7.52	3.49	2.38	135	-8.5	-15.2	-28.1
	30-Jul	22.0	7.56	2.11	4.11	188	-3.6	-9.8	-28.2
	11-Sep	19.0	7.46	4.90	1.96	97	-17.7	-25.2	-27.2
En Coeur	23-May	11.9	6.57	1.48	0.94	-47	-7.4	-15.4	-26.7
	9-Jun	17.7	6.92	2.56	1.50	199	-8.9	-15.6	-26.9
	4-Jul	23.5	7.40	1.82	2.02	132	-8.1	-14.43	-27.3
	2-Aug	22.2	7.26	0.76	1.91	-5	-6.4	-12.8	-27.0
	8-Sep	19.0	7.33	1.52	1.29	-10	-5.9	-13.0	-27.9
Gervais	15-May	9.8	6.60	0.44	0.70	-78	-7.3	-15.6	-28.4
	10-Jun	17.0	6.55	4.35	1.74	313	-5.5	-12.6	-29.0
	2-Jul	23.0	6.97	7.19	2.77	176	-5.0	-11.4	-27.6
	29-Jul	20.7	7.21	3.09	2.53	295	-1.7	-8.1	-28.5
	12-Sep	19.5	7.70	1.96	3.28	199	-3.6	-9.7	-28.7
	28-Oct	9.1	7.35	1.05	1.82	401	-4.6	-9.9	-27.2
Montagne Noire	15-May	9.1	6.77	0.94	0.92	-3	-10.6	-17.7	-27.6
	16-Jun	15.0	5.93	3.00	1.64	239	-6.7	-13.7	-27.1
	7-Jul	22.2	6.23	1.53	1.71	173	-5.8	-12.4	-27.1
	1-Aug	20.8	7.17	4.07	6.64	115	-4.5	-10.4	-27.3
	9-Sep	17.4	7.13	1.38	5.14	252	-3.5	-7.8	-26.7
	27-Oct	7.7	7.09	0.80	2.88	47	-6.3	-11.3	-27.3
du Nord	20-May	15.9	7.09	0.94	0.69	-14	-7.4	-14.5	-27.8
	18-Jun	19.0	6.12	2.59	1.30	178	-11.6	-18.5	-28.3
	4-Jul	23.2	6.90	1.92	2.63	255	-10.7	-16.3	-28.1
	1-Aug	22.5	7.44	1.54	2.42	151	-5.5	-11.4	-27.3

	11-Sep	18.0	7.31	0.89	3.86	80	-8.0	-13.3	-27.7
	19-Oct	6.2	7.63	1.08	1.45	533	-8.7	-12.6	-27.7
Ouimet	12-May	10.3	6.92	2.70	0.87	77	-5.8	-13.2	-27.1
	10-Jun	18.0	6.46	3.77	1.16	132	-5.4	-13.0	-27.1
	4-Jul	22.5	6.10	3.12	1.84	168	-6.9	-13.9	-26.4
	29-Jul	21.5	6.10	1.88	2.03	68	-1.7	-8.7	-27.1
	12-Sep	19.0	6.10	1.64	5.20	201	-5.8	-11.4	-27.0
	28-Oct	7.7	7.10	1.65	3.45	734	-5.1	-9.4	-27.5
Pin Rouge	29-May	16.9	6.78	0.99	0.81	14	-14.1	-20.8	-27.5
	17-Jun	17.0	7.48	3.16	0.94	189	-10.7	-17.8	-27.1
	7-Jul	25.0	6.69	5.69	2.14	413	-8.4	-15.2	-27.6
	1-Aug	22.0	6.52	1.26	2.77	95	-5.4	-11.4	-27.8
	8-Sep	18.0	6.52	1.14	1.22	95	-6.6	-13.6	-27.9
	27-Oct	5.4	6.52	0.60	1.40	-49	-3.7	-11.2	-28.0
Rouge	15-May	9.3	6.23	0.97	1.37	97	-8.5	-14.7	-28.0
	11-Jun	16.2	7.69	4.99	0.56	263	-11.6	-19.2	-28.0
	1-Jul	22.2	6.24	0.27	2.31	-67	-8.7	-15.2	-27.3
	5-Aug	23.0	6.86	0.49	1.62	416	-7.4	-10.9	-28.0
	9-Sep	19.0	6.41	0.64	1.70	10	-7.2	-13.0	-27.5
	27-Oct	7.9	6.54	0.92	1.98	41	-8.7	-14.5	-27.6
des Sables	14-May	9.7	6.54	2.53	1.22	190	-8.0	-15.0	-26.3
	9-Jun	16.7	6.03	3.30	1.86	308	-8.5	-15.1	-26.3
	3-Jul	22.7	6.32	0.77	1.52	514	-8.7	-14.1	-27.2
	5-Aug	21.7	6.54	1.12	1.71	172	-5.4	-11.4	-26.6
	10-Sep	18.0	6.28	1.30	2.01	215	-6.8	-12.8	-28.0
	26-Oct	6.8	6.43	1.96	4.15	273	-6.4	-11.3	-28.2
St. Joseph	22-May	13.8	6.55	0.96	2.28	77	-15.4	-20.8	-27.5
	16-Jun	18.5	5.81	1.68	1.73	156	-10.9	-17.0	-27.3
	3-Jul	23.2	6.41	0.38	0.41	23	-11.6	-18.4	-26.7
	5-Aug	22.4	7.71	0.76	0.99	75	-11.6	-18.0	-27.5
	10-Sep	18.0	8.02	0.86	1.77	267	-8.6	-13.7	-28.0
	26-Oct	6.7	7.77	0.83	1.69	283	-11.6	-15.9	-27.5
Tremblent	12-May	4.8	7.50	0.58	0.77	-9	-13.0	-18.5	-25.0
	12-Jun	12.7	6.69	0.57	0.96	-18	-14.3	-20.4	-23.6
	2-Jul	21.0	6.91	0.63	3.63	6	-13.2	-19.0	-24.3
	6-Aug	22.0	6.67	0.41	0.87	115	-11.6	-16.8	-24.7
	12-Sep	19.0	6.43	0.52	1.26	203	-8.0	-12.5	-27.5
	28-Oct	9.3	5.98	0.61	1.59	349	-12.0	-15.1	-27.0
Truite	14-May	9.0	7.41	6.05	5.27	124	-4.3	-11.8	-26.9
	9-Jun	16.3	7.71	8.32	1.65	494	-4.9	-12.5	-27.1
	3-Jul	22.2	7.87	3.55	2.26	302	-11.1	-18.4	-26.3
	3-Aug	21.5	8.08	2.89	1.68	42	-3.5	-11.1	-26.5
	10-Sep	17.7	7.26	2.33	4.38	170	-4.9	-11.6	-27.6
	26-Oct	7.3	7.03	3.40	4.89	331	-1.4	-8.0	-27.3
d'Argent	27-May	15.9	7.91	3.11	1.82	403	-2.0	-10.0	-28.7
	22-Jul	22.0	7.76	2.26	5.17	437	-5.6	-12.6	-28.5
	2-Nov	7.5	7.84	1.41	4.34	301	-0.8	-8.4	-29.0
Bowker	27-May	12.0	7.63	2.00	1.46	74	-5.5	-13.4	-28.1
	22-Jul	21.0	7.17	1.56	1.78	61	-5.4	-12.6	-28.3
	2-Nov	8.6	7.09	1.11	1.57	-26	-5.3	-13.8	-28.7

Brome	28-May	15.0	8.57	2.15	0.71	45	-4.1	-11.9	-28.4
	23-Jul	22.1	7.6	3.36	2.86	162	-4.1	-10.4	-28.0
	3-Nov	8.1	7.15	4.57	2.43	31	-4.1	-10.8	-28.2
Orford	27-May	13.7	8.37	5.43	3.14	73	-3.7	-11.1	-27.7
	22-Jul	22.0	8.57	3.58	3.55	187	-2.6	-9.6	-28.7
	2-Nov	8.4	7.34	1.74	3.76	425	-1.5	-8.5	-28.4
Waterloo	28-May	15.8	7.98	9.62	1.97	74	-3.0	-11.6	-28.7
	23-Jul	22.7	7.63	6.46	1.14	-1	-0.3	-8.1	-28.9
	3-Nov	7.2	7.39	4.46	3.34	63	2.5	-4.9	-28.3
la Peche	3-Jun	14.7	8.1	3.97	4.03	273	-2.8	-10.3	-27.4
	25-Jul	22.4	8.79	3.97	0.84	152	-1.6	-9.1	-27.7
	31-Oct	9.0	7.46	5.29	4.31	274	-0.4	-8.1	-27.2
Phillippe	3-Jun	14.9	7.61	4.79	1.54	76	-1.9	-10.1	-27.4
	25-Jul	21.9	7.99	3.71	2.02	16	-1.9	-9.8	-27.5
	31-Oct	9.1	7.46	2.63	3.52	353	-1.9	-9.5	-27.8

Appendix 7 Oxygen and volume profiles of lakes sampled in 2003

Table A7- 13. Oxygen profiles (mg L^{-1}) and volume profiles of lakes sampled in 2003 as used to calculate NEP (GPP-R) in the whole lake.

Achigan		16-May	11-Jun	30-Jun	30-Jul	2-Sep	13-Nov
e_z		4	4	3.5	5.5	5.5	
Epilimnetic Respiration (mg C m^{-3} d^{-1})		58.8	63.3	83.1	36.3	20.1	27.9
Epilimnetic Production (mg C m^{-3} d^{-1})		40.3	56.9	88.1	31.2	30.0	19.3
Depth	Volume	16-May	11-Jun	30-Jun	30-Jul	2-Sep	13-Nov
0 to 1	5308958	11.80	10.32	8.92	10.57	9.24	10.33
1 to 2	4900576	11.78	10.32	8.90	10.50	9.37	10.29
2 to 3	4968392	11.77	10.31	8.83	10.46	9.37	10.25
3 to 4	4586208	11.76	10.28	8.74	10.42	9.35	10.22
4 to 5	4527455	11.73	10.43	9.42	10.38	9.35	10.19
5 to 6	4179189	11.66	10.51	10.10	10.33	9.26	10.20
6 to 7	4104207	11.63	10.65	10.55	10.62	9.22	10.21
7 to 8	3788498	11.58	10.63	10.24	10.71	8.98	10.21
8 to 9	3767264	11.42	10.52	10.06	10.26	8.79	10.20
9 to 10	3477474	11.39	10.50	9.93	9.94	8.16	10.21
10 to 11	3369708	11.36	10.46	9.79	9.69	7.47	10.21
11 to 12	3110499	11.33	10.43	9.71	9.62	7.27	10.22
12 to 13	2787864	11.33	10.41	9.68	9.54	7.37	10.23
13 to 14	2573413	11.31	10.48	9.67	9.57	7.38	10.24
14 to 15	2328505	11.30	10.51	9.93	9.64	7.29	10.25
15 to 16	2149389	11.24	10.55	9.98	9.70	7.42	10.25
16 to 17	1774529	11.17	10.54	9.87	9.42	7.34	10.24
17 to 18	1638027	10.97	10.38	9.62	9.13	6.60	10.25
18 to 19	1141997	10.76	10.14	9.32	7.87	4.00	10.25
19 to 20	1054151	10.73	9.44	8.94	6.61	2.77	10.25
20 to 21	415935	10.69	9.16	8.11	5.54	1.89	10.24
21 to 22	383940	10.50	9.03	8.22	4.46	1.01	10.24
22 to 23	46970	10.30	8.89	7.58	4.00	0.94	10.23
23 to 24	43356	10.13	8.71	6.79	3.54	0.87	10.22
24 to 25	6549	9.96	8.53	6.50	3.08	0.71	10.21
25 to 26	6046	9.79	8.35	5.86	2.62	0.54	10.20
26 to 27	159	9.62	8.17	5.22	2.16	0.00	10.20
Hypolimnion NEP (mg C d^{-1})			-441268320	-405105771	-84086044	-6.830E8	0
Epilimnion NEP (mg C d^{-1})			-155223263	110800149	-155056248	3.031E8	-1.315E8
Total NEP (kg C)			-596	-294	-239	-380	-1306
		26	19	30	34	72	181
Average NEP (kg C d^{-1})	-570						
Blanche		15-May	11-Jun	01-Jul	02-Aug	09-Sep	27-Oct
e_z		5	4	2.5	5	7	14

Epilimnetic Respiration (mg C m^{-3} d^{-1})		2.07	73.2	74.4	37.5	30.3	69.5
Epilimnetic Production (mg C m^{-3} d^{-1})		12.5	59.4	81.4	52.0	25.6	30.4
Depth	Volume	15-May	11-Jun	01-Jul	02-Aug	09-Sep	27-Oct
0 to 1	384,485	10.89	9.19	8.80	8.50	8.66	9.92
1 to 2	368,031	10.88	9.22	8.83	8.48	8.65	9.90
2 to 3	350,700	10.86	9.24	9.00	8.48	8.64	9.90
3 to 4	333,217	10.83	9.22	10.32	8.49	8.64	9.88
4 to 5	315,015	10.82	9.20	10.82	8.47	8.64	9.89
5 to 6	295,043	10.80	10.20	11.73	8.60	8.63	9.85
6 to 7	270,997	10.55	10.41	12.56	11.41	8.62	9.87
7 to 8	247,641	10.43	10.47	12.52	11.86	8.62	9.86
8 to 9	229,069	10.23	10.58	12.41	12.18	12.22	9.91
9 to 10	210,628	10.05	10.15	11.72	11.98	12.72	9.90
10 to 11	194,262	10.00	9.60	11.33	11.67	11.76	9.94
11 to 12	182,247	9.80	9.27	10.47	11.23	10.74	9.95
12 to 13	172,879	9.74	9.13	9.58	10.58	10.11	10.02
13 to 14	164,265	9.63	8.84	9.06	8.90	7.62	9.96
14 to 15	154,934	9.57	8.47	8.68	7.87	6.62	9.78
15 to 16	143,165	9.41	8.33	8.30	6.92	5.88	4.64
16 to 17	129,796	9.30	8.06	7.97	5.97	4.71	2.95
17 to 18	115,603	8.95	7.79	7.63	5.02	3.92	1.90
18 to 19	97,528	8.78	7.52	7.51	4.07	3.14	1.37
19 to 20	79,908	8.37	7.25	7.39	3.12	2.57	1.37
20 to 21	61,237	-1.25	-0.92	2.17	0.96	2.57	-8.83
21 to 22	41,573	-10.87	-9.09	-3.05	-1.20	2.57	-19.03
22 to 23	23,820	-20.49	-17.26	-8.27	-3.36	2.57	0.00
23 to 24	13,724	-30.11	-25.43	-13.49	0.00	0.00	0.00
24 to 25	7,408	-39.73	-33.60	-18.71	0.00	0.00	0.00
25 to 26	2,621	-49.35	-41.77	-23.93	0.00	0.00	0.00
26 to 27	0	-58.97	-49.94	-29.15	0.00	0.00	0.00
Hypolimnion NEP (mg C d^{-1})			-17022675	55174004	-17878764	-7970564	-6168511
Epilimnion NEP (mg C d^{-1})			-19880229	6467226	29694576	-11979152	-1.513 E7
Total NEP (kg C)			-37	62	12	-20	-157
		27	20	32	38	48	
Average NEP (kg C d^{-1})	-24						

Connelly		16-May	11-Jun	30-Jun	30-Jul	02-Sep
e_z		3.0	3.0	3.0	3.0	5.0
Epilimnetic Respiration (mg C m^{-3} d^{-1})		56.4	79.8	119.4	57	74.1
Epilimnetic Production (mg C m^{-3} d^{-1})		59.9	82.9	104.0	54.1	60.5
Depth	Volume	16-May	11-Jun	30-Jun	30-Jul	02-Sep
0 to 1	1,191,220	10.09	9.14	8.89	10.04	8.96
1 to 2	1,099,587	10.13	9.37	8.81	10.94	8.98
2 to 3	1,028,729	10.10	9.33	8.77	10.85	8.93
3 to 4	949,596	10.14	9.47	8.72	10.79	8.95
4 to 5	873,558	10.96	9.49	11.54	10.86	9.16
5 to 6	806,362	10.83	9.13	9.45	11.07	8.91

6 to 7	597,138	10.10	8.25	8.29	7.93	8.66
7 to 8	551,204	9.54	7.85	7.86	7.46	4.87
8 to 9	439,739	9.12	7.72	7.71	7.03	4.67
9 to 10	405,913	8.81	7.51	7.62	6.46	4.25
10 to 11	354,720	8.49	7.75	6.96	6.39	3.65
11 to 12	327,434	8.32	7.25	6.70	6.19	2.65
12 to 13	261,444	8.14	7.00	6.06	5.33	1.84
13 to 14	241,332	7.98	6.85	5.75	4.58	1.06
14 to 15	176,246	7.81	6.69	5.42	3.83	0.83
15 to 16	162,689	7.78	6.59	5.29	2.93	0.57
16 to 17	33,482	7.74	6.48	4.80	2.03	0.35
17 to 18	30,906	7.70	6.18	4.31	1.50	0.27
18 to 19	14,845	7.66	5.87	3.81	0.97	0.20
19 to 20	13,703	7.62	5.67	3.41	0.26	0.04
20 to 21	848.64	7.59	5.46	3.01	0.00	0.00
21 to 22	783	7.55	5.26	2.60	0.00	0.00
22 to 23	1,632	7.51	5.05	2.20	0.00	0.00

Hypolimnion NEP (mg C d^{-1})		-37201918	-41442860	-23950453	-72024583
Epilimnion NEP (mg C d^{-1})		13277001	-65830015	-12295100	-81026088
Total NEP (kg C)		-24	-107	-36	-153
	26	19	30	34	
Average NEP (kg C d^{-1})	-66				

En Coeur	13-May	09-Jun	04-Jul	02-Aug	08-Sep
e_z	3	4	3	4	
Epilimnetic Respiration (mg C m^{-3} d^{-1})	3.3	38.1	111.3	77.4	87.6
Epilimnetic Production (mg C m^{-3} d^{-1})	23.1	45.4	162.5	86.9	90.8

Depth	Volume	13-May	09-Jun	04-Jul	02-Aug	08-Sep
0 to 1	402842	9.91	9.96	7.77	8.13	9.05
1 to 2	339311	9.90	9.23	7.77	8.11	8.31
2 to 3	257545	9.90	9.37	7.76	8.11	8.28
3 to 4	192259	9.90	9.63	7.82	8.10	8.27
4 to 5	128888	9.61	9.92	10.00	7.91	8.21
5 to 6	90634	8.01	9.11	8.70	6.05	8.21
6 to 7	52115	7.00	4.62	3.24	2.80	8.21
7 to 8	15343	6.00	1.14	1.20	0.45	8.21

Hypolimnion NEP (mg C d^{-1})		-654977.78	-1297896.7	-16174117	
Epilimnion NEP (mg C d^{-1})		8689367	67653681	11275913	-9582530
Total NEP (kg C)		8	66	-5	-10
	27	25	29	37	
Average NEP (kg C d^{-1})	15				

Gervais	13-May	6/12	2-Jul	29-Jul	3-Sep	12-Nov
e_z	3	4	4	6	7	16
Epilimnetic Respiration (mg C m^{-3} d^{-1})	80.4	75.6	108.6	42.9	16.5	18.9

Epilimnetic Production (mg C m^{-3} d^{-1})		77.5	72.5	103.9	40.5	20.1	14.6
Depth	Volume	13-May	6/12	2-Jul	29-Jul	3-Sep	12-Nov
0 to 1	894724.6	11.84	10.45	9.25	9.86	9.23	10.17
1 to 2	894724	11.95	10.31	9.11	9.83	9.22	10.14
2 to 3	894724	11.91	10.27	9.05	9.81	9.23	10.14
3 to 4	894724	11.98	10.24	8.98	9.76	9.22	10.14
4 to 5	894724	12.01	10.26	9.01	9.75	9.22	10.14
5 to 6	773,371	12.05	11.03	10.64	9.72	9.22	10.12
6 to 7	773,371	11.81	12.23	11.90	11.59	9.21	10.13
7 to 8	773,371	11.56	12.35	12.13	11.87	9.51	10.12
8 to 9	773,371	11.42	12.12	12.03	11.51	13.59	10.19
9 to 10	773,371	11.30	12.02	11.82	11.15	13.52	10.18
10 to 11	665,762	11.09	11.93	11.64	10.98	13.19	10.23
11 to 12	665,762	11.08	11.78	11.55	10.63	12.85	10.19
12 to 13	665,762	10.92	11.40	11.33	10.46	12.25	10.30
13 to 14	665,762	10.72	11.22	10.98	10.21	11.70	10.33
14 to 15	665,762	10.51	10.67	10.65	9.97	10.76	10.27
15 to 16	580,163	10.23	10.41	10.32	9.75	10.35	10.28
16 to 17	580,163	9.95	10.08	9.98	9.46	9.75	10.29
17 to 18	580,163	9.87	9.87	9.75	9.16	9.28	10.03
18 to 19	580,163	9.78	9.67	9.55	9.02	8.96	9.76
19 to 20	580,163	9.61	9.50	9.25	8.87	8.60	7.88
20 to 21	502,720	9.43	9.34	9.12	8.69	8.35	7.17
21 to 22	502,720	9.30	9.30	9.01	8.51	8.10	6.94
22 to 23	502,720	9.17	9.26	8.89	8.34	7.91	6.70
23 to 24	502,720	9.04	9.10	8.74	8.17	7.71	6.57
24 to 25	502,720	8.99	8.93	8.59	8.00	7.56	6.44
25 to 26	422,873	8.94	8.89	8.54	7.96	7.40	6.33
26 to 27	422,873	8.89	8.85	8.48	7.92	7.33	6.22
27 to 28	422,873	8.86	8.81	8.39	7.88	7.27	6.11
28 to 29	422,873	8.82	8.75	8.30	7.81	7.20	6.00
29 to 30	422,873	8.79	8.68	8.23	7.74	7.14	5.89
30 to 31	327137	8.72	8.61	8.16	7.67	7.07	5.79
31 to 32	327137	8.65	8.61	8.16	7.67	7.07	5.79
32 to 33	327137	8.58	8.61	8.16	7.67	7.07	5.79
33 to 34	327137	8.50	8.61	8.16	7.67	7.07	5.79
34 to 35	327137	8.42	8.61	8.16	7.67	7.07	5.79
36 to 37	227191	8.34	8.21	7.87	7.51	6.37	5.12
37 to 38	227191	8.34	8.21	7.87	7.51	6.37	5.12
38 to 39	227191	8.34	8.21	7.87	7.51	6.37	5.12
39 to 40	227191	8.34	8.21	7.87	7.51	6.37	5.12
40 to 41	227191	8.34	8.21	7.87	7.51	6.37	5.12
41 to 42	158995	8.07	7.74	7.40	6.67	5.50	3.70
42 to 43	158995	8.07	7.74	7.40	6.67	5.50	3.70
43 to 44	158995	8.07	7.74	7.40	6.67	5.50	3.70
44 to 45	158995	8.07	7.74	7.40	6.67	5.50	3.70
45 to 46	158995	8.07	7.74	7.40	6.67	5.50	3.70
46 to 47	94982	7.75	7.41	6.60	5.78	4.25	3.32
47 to 48	94982	7.75	7.41	6.60	5.78	4.25	3.32

48 to 49	94982	7.75	7.41	6.60	5.78	4.25	3.32
49 to 50	94982	7.75	7.41	6.60	5.78	4.25	3.32
50 to 51	94982	7.75	7.41	6.60	5.78	4.25	3.32
51 to 52	47406	7.29	6.67	5.71	4.62	2.68	1.40
52 to 53	47406	7.29	6.67	5.71	4.62	2.68	1.40
53 to 54	47406	7.29	6.67	5.71	4.62	2.68	1.40
54 to 55	47406	7.29	6.67	5.71	4.62	2.68	1.40
55 to 56	47406	7.29	6.67	5.71	4.62	2.68	1.40
56 to 57	9843	5.67	5.55	4.53	2.60		0.66
Hypolimnion NEP (mg C d^{-1})			22920975	-83783585	-112428270	23129990	-58097923
Epilimnion NEP (mg C d^{-1})			-13912968	-20936556	-12540316	24593324	-44142252
Total NEP (kg C)			-4	-63	-282	48	844
		30	20	27	36	70	
Average NEP (kg C d^{-1})	97						

Montagne Noire	15-May	16-Jun	7-Jul	1-Aug	9-Sep	27-Oct
e_z	6.00	6.00	4.00	7.00	8.50	
Epilimnetic Respiration (mg C m^{-3} d^{-1})	31.5	109.5	46.2	40.2	43.2	18.6
Epilimnetic Production (mg C m^{-3} d^{-1})	36.1	83.7	58.7	54.3	35.0	12.4

Depth	Volume	15-May	16-Jun	7-Jul	1-Aug	9-Sep	27-Oct
0 to 1	250,752	12.47	9.91	8.30	8.60	8.63	9.59
1 to 2	208,059	12.55	9.92	8.30	8.59	8.63	9.54
2 to 3	165,365	12.55	10.07	8.29	8.57	8.62	9.54
3 to 4	138,319	12.59	10.08	8.28	8.56	8.62	9.52
4 to 5	128,853	12.68	10.11	8.28	8.53	8.60	9.51
5 to 6	119,387	12.72	10.08	8.49	8.61	8.59	9.50
6 to 7	149,138	12.66	10.09	10.55	8.77	8.59	9.50
7 to 8	147,978	12.31	10.50	10.94	9.40	8.54	9.49
8 to 9	146,819	12.05	10.95	11.49	10.88	8.52	9.55
9 to 10	186,615	11.88	11.04	11.89	12.00	8.52	9.53
10 to 11	185,263	11.78	10.88	12.21	12.00	11.13	9.60
11 to 12	183,911	11.52	10.34	12.05	11.64	10.77	9.63
12 to 13	183,138	11.33	10.39	11.14	10.50	9.57	9.67
13 to 14	181,013	11.07	10.31	10.08	9.52	7.95	9.65
14 to 15	178,888	10.90	9.80	9.88	8.67	7.39	9.70
15 to 16	142,376	10.85	9.51	9.43	8.25	6.89	9.70
16 to 17	142,376	10.85	9.42	9.32	7.95	6.59	9.77
17 to 18	142,376	10.85	8.91	8.93	7.83	5.87	9.73
18 to 19	142,376	10.85	8.91	8.93	7.83	5.17	9.81
19 to 20	142,376	10.85	8.91	8.93	7.83	4.81	9.75
20 to 21	142,376	10.85	8.91	8.93	7.83	4.81	9.24
21 to 22	109,149	10.85	8.91	8.93	7.83	4.81	9.24
22 to 23	109,149	10.85	8.91	8.93	7.83	4.81	9.24
23 to 24	109,149	10.85	8.91	8.93	7.83	4.81	9.24
24 to 25	72,057	10.85	8.91	8.93	7.83	4.81	9.24
25 to 26	72,057	10.85	8.91	8.93	7.83	4.81	9.24
26 to 27	72,057	10.85	8.91	8.93	7.83	4.81	9.24
27 to 28	49841	10.85	8.91	8.93	7.83	4.81	9.24

27 to 28	49841	10.85	8.91	8.93	7.83	4.81	9.24
28 to 29	49841	10.85	8.91	8.93	7.83	4.81	9.24
29 to 30	49841	10.85	8.91	8.93	7.83	0.00	9.24
30 to 31	26466	10.85	8.91	8.93	7.83	0.00	9.24
31 to 32	26466	10.85	8.91	8.93	7.83	0.00	9.24
32 to 33	26466	10.85	8.91	8.93	0.00	0.00	9.24
33 to 34	19704	10.85	8.91	8.93	0.00	0.00	9.24
Hypolimnion NEP (mg C d^{-1})			-55978297	-3005475.4	-37577151	-29227911	
Epilimnion NEP (mg C d^{-1})			-29913126	11141852	18479942	-13458546	-55434262
Total NEP (kg C)			-86	8	-19	-43	-55
		32	21	25	39	48	
Average NEP (kg C d^{-1})	-44						

du Nord		10-May	18-Jun	04-Jul	01-Aug	11-Sep	19-Oct
e_z		4	3	3	3	5	
Epilimnetic Respiration (mg C m^{-3} d^{-1})		80.4	73.2	78.9	60	108	12.6
Epilimnetic Production (mg C m^{-3} d^{-1})		82.4	90.3	134.4	93.3	98.9	9.0
Depth	Volume	10-May	18-Jun	04-Jul	01-Aug	11-Sep	19-Oct
0 to 1	832,780	9.97	8.77	7.59	8.34	8.70	9.72
1 to 2	750,484	10.01	8.77	7.59	8.33	8.60	9.75
2 to 3	656,868	9.96	9.22	7.58	8.33	8.65	9.72
3 to 4	533,369	9.91	9.06	7.57	8.41	8.63	9.66
4 to 5	464,351	9.95	8.66	8.08	8.22	8.48	9.68
5 to 6	418,052	9.73	7.70	6.80	6.40	7.70	9.64
6 to 7	366,558	9.01	7.16	6.14	5.00	5.99	9.67
7 to 8	277,148	8.76	6.74	5.81	4.48	1.40	9.66
8 to 9	214,078	8.77	6.67	5.70	4.34	2.04	9.72
9 to 10	189,405	8.50	6.62	5.71	4.67	3.52	9.69
10 to 11	169,478	8.29	6.15	5.60	4.59	3.78	9.77
11 to 12	150,713	8.26	5.89	5.15	4.17	4.12	9.75
12 to 13	131,562	8.24	5.52	4.70	3.55	3.43	9.80
13 to 14	111,175	8.23	5.23	4.37	3.01	3.12	9.78
14 to 15	89,053	8.21	4.94	3.92	0.46	3.37	9.85
15 to 16	65,234	8.00	4.65	3.47	0.00	1.19	9.84
16 to 17	41,522	7.48	4.36	3.02	0.00	0.35	9.83
17 to 18	26,702	7.29	4.07	2.60	0.00	0.00	9.84
18 to 19	16,993	7.10	3.78	2.18	0.00	0.00	9.85
19 to 20	7,652	6.91	3.49	1.76	0.00	0.00	9.85
20 to 21	870	6.72	3.20	1.34	0.00	0.00	9.86
Hypolimnion NEP (mg C d^{-1})			-43949545	-44441272	-24204506	-3711657	
Epilimnion NEP (mg C d^{-1})			47426870	153790640	92385324	-33414971	-40401107
Total NEP (kg C)			3	109	68	-37	-40
		39	16	28	41	38	
Average NEP (kg C d^{-1})	17						

Ouimet		13-May	12-Jun	02-Jul	29-Jul	03-Sep	12-Nov
e_z		2.00	3.00	3.00	4.00	5.00	
Epilimnetic Respiration (mg C m^{-3} d^{-1})		48.9	84.9	99	45.3	57.6	34.2
Epilimnetic Production (mg C m^{-3} d^{-1})		60.3	78.3	123.1	47.7	62.6	25.9
Depth	Volume	13-May	12-Jun	02-Jul	29-Jul	03-Sep	12-Nov
0 to 1	224,990	12.01	9.78	8.97	10.21	9.32	10.02
1 to 2	224,990	12.24	9.86	8.87	9.90	9.33	9.99
2 to 3	226,710	12.19	9.83	8.82	9.82	9.34	9.96
3 to 4	228,431	11.89	9.80	8.69	9.73	9.35	9.95
4 to 5	228,431	11.64	10.46	9.82	9.67	9.35	9.94
5 to 6	257,763	11.49	11.32	11.14	10.62	9.28	9.94
6 to 7	257,763	10.94	11.62	11.92	11.57	9.82	9.93
7 to 8	201,639	10.69	10.94	11.81	11.41	11.47	9.92
8 to 9	145,514	10.34	9.81	9.37	8.96	9.59	9.91
9 to 10	145,514	9.80	9.39	8.50	7.38	6.33	9.94
10 to 11	157,968	9.32	9.27	8.17	6.92	5.26	9.96
11 to 12	157,968	9.07	8.94	8.03	6.95	5.19	9.96
12 to 13	131,422	8.81	8.61	7.90	6.97	5.11	9.96
13 to 14	104,875	8.65	8.44	7.71	6.78	5.23	9.96
14 to 15	104,875	8.48	8.27	7.51	6.58	5.34	9.96
15 to 16	94,879	8.37	8.12	7.13	6.90	5.76	9.96
16 to 17	94,879	8.26	7.97	6.75	7.21	6.17	9.96
17 to 18	96,190	7.93	7.49	6.38	6.47	5.39	9.96
18 to 19	97,501	7.59	7.01	6.02	5.73	4.60	9.96
19 to 20	97,501	7.24	6.53	5.65	5.00	3.64	9.96
20 to 21	211,389	6.89	5.76	4.15	3.91	2.69	9.96
21 to 22	211,389	6.36	5.00	2.65	2.83	1.73	9.96
22 to 23	159,377	5.82	4.23	1.14	1.74	0.78	9.96
Hypolimnion NEP (mg C d^{-1})			-13194373	-37946461	-13244556	-23115341	
Epilimnion NEP (mg C d^{-1})			-5991900	21786259	2743195	-7876673	-2.330E8
Total NEP (kg C)			-19	-16	-11	-31	-233
		30	20	27	36	70	
Average NEP (kg C d^{-1})	-62						
Pin Rouge		29-May	17-Jun	07-Jul	01-Aug	08-Sep	27-Oct
e_z		1.00	1.00	1.00	1.00	3.00	
Epilimnetic Respiration (mg C m^{-3} d^{-1})		111.9	119.1	85.2	88.8	99	42
Epilimnetic Production (mg C m^{-3} d^{-1})		224.6	113.0	185.4	144.5	105.7	27.5
Depth	Volume	29-May	17-Jun	07-Jul	01-Aug	08-Sep	27-Oct
0 to 1	132634.32	10.07	8.76	7.66	8.23	8.64	8.74
1 to 2	122431.68	10.10	9.15	7.80	8.30	8.72	8.74
2 to 3	100388.6	10.00	8.29	7.39	8.58	8.67	8.72
3 to 4	92666.4	10.55	5.73	6.72	6.30	7.93	8.72
4 to 5	67148.64	9.05	4.53	3.76	2.42	1.07	8.61
5 to 6	61983.36	6.87	5.73	2.53	1.37	0.20	8.56
6 to 7	43060.68	5.82	4.53	1.53	0.85	0.16	8.59

6 to 7	43060.68	5.82	4.53	1.53	0.85	0.16	8.59
7 to 8	39,748	4.50	4.38	0.07	0.12	0.16	8.56
8 to 9	25,927	3.45	3.43	0.05	0.09	0.13	8.29
9 to 10	23,932	1.92	0.61	0.02	0.00	0.09	8.63
10 to 11	12,226	0.73	0.00	0.00	0.00	0.10	0.30
11 to 12	11,285	0.69	0.00	0.00	0.00	0.09	0.27
12 to 13	3,443	0.54	0.00	0.00	0.00	0.09	0.00
13 to 14	3,179	0.00	0.00	0.00	0.00	0.00	0.00
Hypolimnion NEP (mg C d^{-1})		-18850230	-12242903	-1603342	-1247823.6	73862.758	
Epilimnion NEP (mg C d^{-1})		-803764	13291285	19798821	24411462	-10293855	
Total NEP (kg C)		-20	1	18	23	-10	
		19	20	25	63	49	
Average NEP (kg C d^{-1})	7						
Rouge		15-May	11-Jun	01-Jul	05-Aug	09-Sep	27-Oct
e_z		3	4	4	6	7	
Epilimnetic Respiration (mg C m^{-3} d^{-1})		22.8	48	70.2	42.9	46.8	27
Epilimnetic Production (mg C m^{-3} d^{-1})		29.8	51.8	71.2	64.5	37.5	12.9
Depth	Volume	15-May	11-Jun	01-Jul	05-Aug	09-Sep	27-Oct
0 to 1	647572.09	11.13	9.62	8.28	8.46	8.61	9.24
1 to 2	593235.27	11.09	9.65	8.28	8.50	8.56	9.18
2 to 3	555727.2	11.16	9.65	8.27	8.63	8.55	9.15
3 to 4	524854.8	10.98	9.68	8.25	8.72	8.56	9.14
4 to 5	493748.68	10.83	9.69	8.25	8.76	8.59	9.16
5 to 6	456462.05	10.50	10.17	10.06	8.72	8.58	9.13
6 to 7	414457.88	10.15	10.35	10.81	8.80	8.55	9.16
7 to 8	357365.75	9.83	10.55	11.33	11.08	8.49	9.14
8 to 9	293087.52	9.61	10.46	11.54	11.28	8.24	9.17
9 to 10	232075.71	9.27	8.89	9.95	9.56	7.13	9.18
10 to 11	185850.99	9.11	8.43	7.45	6.22	4.60	9.20
11 to 12	151212.69	8.67	7.78	6.75	5.22	2.53	9.20
12 to 13	116364.05	8.64	7.52	6.51	4.72	1.84	9.18
13 to 14	86397.758	8.30	7.35	6.33	4.63	1.77	9.10
14 to 15	64134.334	8.20	7.08	6.12	4.62	1.31	8.55
15 to 16	49209.757	8.07	7.00	5.84	4.20	0.74	8.29
16 to 17	36777.038	7.90	6.05	5.62	4.03	0.30	7.92
17 to 18	27631.742	7.88	5.89	5.40	3.86	0.00	7.79
18 to 19	19941.359	7.54	5.49	5.18	3.69	0.00	0.40
19 to 20	12907.248	7.44	5.09	4.96	3.52	0.00	0.00
20 to 21	6083.1373	7.23	4.69	4.74	3.35	0.00	0.00
21 to 22	1765.1187	7.08	4.29	4.52	3.18	0.00	0.00
22 to 23	56.141434	6.92	3.89	4.30	3.01	0.00	0.00
Hypolimnion NEP (mg C d^{-1})			-5134711.7	4245762.7	-12071142	-30141959	
Epilimnion NEP (mg C d^{-1})			10556768	2927744	79766294	-37603841	-84892023
Total NEP (kg C)			5	7	68	-68	-85
		27	20	35	35	48	
Average NEP (kg C d^{-1})	-13						

des Sables		14-May	09-Jun	03-Jul	05-Aug	10-Sep	26-Oct
e_z		3	3	4	5	8	
Epilimnetic Respiration (mg C m^{-3} d^{-1})		33	46.2	81.6	52.5	58.8	30.3
Epilimnetic Production (mg C m^{-3} d^{-1})		43.0	47.3	76.6	77.9	56.1	21.1
Depth	Volume	14-May	09-Jun	03-Jul	05-Aug	10-Sep	26-Oct
0 to 1	782,801	10.30	9.50	7.89	8.51	8.38	9.93
1 to 2	782,801	10.33	9.58	7.79	8.53	8.32	9.89
2 to 3	782,801	10.36	9.69	7.93	8.54	8.30	9.86
3 to 4	759,080	10.36	9.68	8.07	8.59	8.29	9.84
4 to 5	759,080	10.31	9.86	8.04	8.60	8.28	9.83
5 to 6	759,080	10.10	9.95	9.71	8.47	8.25	9.74
6 to 7	615,206	9.54	9.92	9.93	8.26	8.19	9.33
7 to 8	615,206	9.30	9.56	9.61	9.77	8.05	9.80
8 to 9	615,206	9.00	9.48	8.80	9.98	7.42	9.85
9 to 10	317,143	8.78	8.45	8.14	8.74	5.36	9.83
10 to 11	317,143	8.65	8.19	7.31	7.05	4.33	10.14
11 to 12	317,143	8.60	7.85	6.90	5.88	3.57	10.14
12 to 13	207,819	8.53	7.50	6.52	5.23	2.82	10.14
13 to 14	207,819	8.29	7.58	6.10	4.82	2.28	10.14
14 to 15	207,819	8.12	7.33	5.94	4.29	1.78	10.14
15 to 16	150,578	8.03	7.22	5.34	3.76	1.27	10.14
16 to 17	150,578	7.93	7.00	4.98	3.23	0.39	10.14
17 to 18	150,578	7.86	6.77	4.37	2.70	0.00	10.14
18 to 19	80,446	7.73	6.55	3.99	2.17	0.00	10.14
19 to 20	80,446	7.59	6.32	3.60	1.64	0.00	10.14
20 to 21	80,446	7.46	6.10	3.22	1.11	0.00	10.14
21 to 22	46,927	7.32	5.88	2.83	0.58	0.00	10.14
22 to 23	46,927	7.19	5.65	2.45	0.05	0.00	10.14
23 to 24	46,927	7.06	5.43	2.07	0.00	0.00	10.14
Hypolimnion NEP (mg C d^{-1})			-19075125	-49258384	-24913318	-48766688	
Epilimnion NEP (mg C d^{-1})			3480382	-19526151	117630142	-17731256	-2.021E8
Total NEP (kg C)			-16	-69	93	-66	-202
		26	24	33	36	46	165
Average NEP (kg C d^{-1})	-41						

St. Joseph		22-May	16-Jun	3-Jul	5-Aug	10-Sep	26-Oct
e_z		5	5	3	4	6	
Epilimnetic Respiration (mg C m^{-3} d^{-1})		43.5	116.1	66.6	62.7	74.4	3
Epilimnetic Production (mg C m^{-3} d^{-1})		34.8	102.0	158.5	93.9	64.8	4.7
Depth	Volume	22-May	16-Jun	3-Jul	5-Aug	10-Sep	26-Oct
0 to 1	341286	9.71	8.92	8.12	8.34	8.32	9.35
1 to 2	329415	9.82	8.99	8.12	8.37	8.30	9.30
2 to 3	318534	9.84	9.31	8.15	8.35	8.28	9.23
3 to 4	354227	9.81	9.56	8.14	8.47	8.27	9.18
4 to 5	341906	9.80	9.49	8.67	8.16	8.24	9.11
5 to 6	330612	9.79	9.22	9.83	8.07	8.16	9.05

7 to 8	189077	9.55	8.76	8.35	7.85	6.76	9.04
8 to 9	182831	9.29	8.78	8.22	7.66	5.68	9.07
9 to 10	148440	9.19	8.64	8.20	7.58	5.77	9.08
10 to 11	143277	9.08	8.53	7.99	7.53	5.74	9.12
11 to 12	138544	8.99	8.51	7.88	7.37	5.65	9.13
12 to 13	147172	9.00	8.52	7.88	7.31	5.61	9.14
13 to 14	142053	9.92	8.56	7.85	7.23	5.53	9.15
14 to 15	137360	8.91	8.61	7.85	7.14	5.52	9.32
15 to 16	110886	8.92	8.55	7.82	7.06	5.48	8.24
16 to 17	107029	8.91	8.59	7.78	6.97	5.47	8.22
17 to 18	103494	8.89	8.57	7.75	6.88	5.44	6.54
18 to 19	97184	8.84	8.56	7.71	6.79	5.40	5.96
19 to 20	93804	8.82	8.54	7.68	6.71	5.37	4.36
20 to 21	90705	8.81	8.52	7.64	6.62	5.33	3.98
21 to 22	64197	8.79	8.50	7.61	6.53	5.30	3.13
22 to 23	61964	8.77	8.49	7.57	6.44	5.26	2.27
24 to 25	59917	8.75	8.47	7.54	6.36	5.23	1.60
25 to 26	30703	8.74	8.45	7.50	6.27	5.19	0.38
26 to 27	29635	8.72	8.43	7.47	6.18	5.16	0.85
27 to 28	28656	8.70	8.42	7.43	6.09	5.12	0.85
28 to 29	24359	8.68	8.40	7.40	6.01	5.09	0.67
29 to 30	23512	8.67	8.38	7.36	5.92	5.05	1.22
30 to 31	22735	8.65	8.36	7.33	5.83	5.02	0.00
31 to 32	7105	8.63	8.35	7.29	5.74	4.98	0.00
32 to 33	6858	8.61	8.33	7.26	5.65	4.95	0.00
33 to 34	6631	8.60	8.31	7.22	5.57	4.91	0.00

Hypolimnion NEP (mg C d^{-1})		-14548423	-29821041	-20820622	-27466160	
Epilimnion NEP (mg C d^{-1})		-28445463	123490966	52617166	-21167591	-6888862
Total NEP (kg C)		-43	94	32	-49	-7
	25	17	33	36	46	
Average NEP (kg C d^{-1})	-1					

Tremblant	13-May	12-Jun	02-Jul	29-Jul	03-Sep	12-Nov
e_z		9	4	7	9	
Epilimnetic Respiration (mg C m^{-3} d^{-1})	7.5	10.8	34.5	15	21.3	22.5
Epilimnetic Production (mg C m^{-3} d^{-1})	6.6	15.4	43.0	39.5	19.5	14.4

Depth	Volume	13-May	12-Jun	02-Jul	29-Jul	03-Sep	12-Nov
0 to 1	2,173,744	12.00	10.82	9.44	9.74	9.03	10.68
1 to 2	2,173,744	12.10	10.81	9.32	9.64	9.03	10.67
2 to 3	2,173,744	12.10	10.79	9.25	9.62	9.02	10.66
3 to 4	2,173,744	12.08	10.80	9.25	9.61	9.02	10.66
4 to 5	2,173,744	12.02	10.81	9.24	9.61	9.02	10.66
5 to 6	2,173,744	12.02	10.88	9.85	9.60	8.99	10.66
6 to 7	2,173,744	12.09	10.94	10.38	9.62	8.95	10.66
7 to 8	1,956,304	12.09	11.01	10.48	9.62	8.94	10.66
8 to 9	1,650,778	12.07	11.05	10.56	9.89	8.92	10.66
	1,650,778	12.06	11.12	10.6	10.35	8.8	10.66
9 to 10							

				3		5	
10 to 11	1,650,778	12.05	11.21	10.73	10.23	9.11	10.65
11 to 12	1,650,778	12.03	11.33	10.78	10.29	9.45	10.65
12 to 13	1,650,778	12.02	11.40	10.84	10.31	9.50	10.65
13 to 14	1,650,778	12.00	11.42	10.89	10.30	9.56	10.65
14 to 15	1,650,778	11.99	11.44	10.86	10.37	9.74	10.65
15 to 16	1,819,166	11.98	11.46	10.92	10.44	9.64	10.65
16 to 17	1,863,928	11.98	11.53	10.94	10.44	9.58	10.65
17 to 18	1,863,928	11.97	11.55	10.95	10.43	9.68	10.65
18 to 19	1,863,928	11.97	11.55	11.00	10.43	9.78	10.65
19 to 20	1,863,928	11.97	11.57	10.98	10.42	9.91	10.66
20 to 21	1,863,928	11.97	11.57	11.04	10.45	10.04	10.67
21 to 22	1,863,928	11.96	11.59	11.07	10.48	10.09	10.67
22 to 23	1,759,893	11.96	11.60	11.10	10.49	10.14	10.66
24 to 25	1,301,575	11.95	11.61	11.13	10.50	10.19	10.65
25 to 26	1,301,575	11.96	11.61	11.16	10.52	10.21	10.63
26 to 27	1,301,575	11.96	11.62	11.18	10.52	10.23	10.64
27 to 28	1,301,575	11.96	11.63	11.19	10.53	10.25	10.64
28 to 29	1301575	11.95	11.63	11.19	10.53	10.25	10.64
29 to 30	1301575	11.96	11.63	11.19	10.54	10.25	10.64
30 to 31	1301575	11.96	11.63	11.20	10.55	10.26	10.62
31 to 32	1172687	11.95	11.63	11.20	10.55	10.26	10.60
32 to 33	1079354	11.95	11.63	11.21	10.55	10.29	10.59
33 to 34	1079354	11.95	11.63	11.22	10.55	10.32	10.58
34 to 35	1079354	11.95	11.65	11.23	10.55	10.35	10.57
35 to 36	1079354	11.95	11.65	11.24	10.55	10.38	10.56
36 to 37	1079354	11.95	11.65	11.24	10.56	10.41	10.56
37 to 38	1079354	11.95	11.65	11.24	10.56	10.41	10.56
38 to 39	1079355	11.95	11.65	11.24	10.56	10.42	10.56
39 to 40	539904	11.95	11.65	11.24	10.56	10.43	10.56
40 to 45	2630361	11.95	11.65	11.24	10.56	10.44	10.56
45 to 50	1591096	11.95	11.65	11.24	10.56	10.44	10.56
50 to 55	1064140	11.95	11.65	11.24	10.56	10.44	10.56
55 to 60	929696	11.95	11.65	11.24	10.56	10.45	10.56
60 to 65	865207	11.95	11.65	11.24	10.56	10.45	10.56
65 to 70	802487	11.95	11.65	11.24	10.56	10.45	10.56
70 to 75	600901	11.95	11.65	11.24	10.56	10.45	10.56
75 to 80	654416	11.95	11.65	11.24	10.56	10.45	10.56
80 to 85	682216	11.95	11.65	11.24	10.56	10.46	10.56
85 to 90	555550	11.95	11.65	11.24	10.56	10.46	10.56
90 to 95	325666	11.95	11.65	11.24	10.56	10.46	10.56
95 to 100	132380	11.95	11.65	11.24	10.56	10.46	10.56
Hypolimnion NEP (mg C d^{-1})			-206901121	-466270353	-372826526	-1.7486E8	
Epilimnion NEP (mg C d^{-1})			93361754	92818875	420898289	-37877027	-9.6418E8
Total NEP (kg C)			-114	-373	48	-213	-964
		30	20	27	36	70	
Average NEP (kg C d^{-1})	-270						

à la Truite		14-May	09-Jun	03-Jul	03-Aug	10-Sep	26-Oct
e_z		3	4	4	4	7	15
Epilimnetic Respiration (mg C m^{-3} d^{-1})		42.9	41.7	33.9	64.8	29.4	49.2
Epilimnetic Production (mg C m^{-3} d^{-1})		46.9	42.3	45.6	110.8	53.8	32.4
Depth	Volume	14-May	09-Jun	03-Jul	03-Aug	10-Sep	26-Oct
0 to 1	493,738	10.80	9.38	8.24	8.79	8.52	10.07
1 to 2	455,683	10.76	9.43	8.27	7.79	8.50	9.94
2 to 3	419,054	10.72	9.43	8.29	8.84	8.52	9.89
3 to 4	391,966	10.71	9.60	8.29	8.88	8.49	9.88
4 to 5	366,572	10.48	9.67	8.26	8.90	8.48	9.86
5 to 6	335,688	10.33	9.78	10.18	8.85	8.47	9.85
6 to 7	296,287	10.00	9.79	10.59	9.00	8.46	9.87
7 to 8	262,753	9.66	9.98	10.36	10.60	8.34	9.74
8 to 9	239,769	9.56	9.85	10.37	10.84	8.63	9.92
9 to 10	218,733	9.54	9.85	9.23	10.96	10.55	9.92
10 to 11	198,847	9.30	8.89	9.50	11.89	10.13	9.95
11 to 12	180,432	9.24	8.45	8.83	9.50	8.54	9.96
12 to 13	162,271	9.05	8.04	8.30	7.31	6.51	10.00
13 to 14	144,964	8.88	7.84	7.54	6.93	5.58	10.00
14 to 15	129,704	8.77	7.56	7.33	6.60	4.54	9.73
15 to 16	114,972	8.64	7.08	6.85	6.15	3.71	7.74
16 to 17	100,896	8.07	6.92	6.73	6.15	2.68	4.00
17 to 18	87,022	7.94	6.59	6.27	5.44	1.60	1.55
18 to 19	72,354	7.81	6.26	5.81	4.73	0.56	0.55
19 to 20	55,857	7.58	5.95	5.49	4.36	0.00	0.00
20 to 21	36,422	7.34	5.64	5.18	3.99	0.00	0.00
21 to 22	17,386	7.11	5.32	4.86	3.61	0.00	0.00
22 to 23	1,202	6.87	5.01	4.54	3.24	0.00	0.00
Hypolimnion NEP (mg C d^{-1})			-16527037	5776349.3	-5132408.8	-27293885	-33095
Epilimnion NEP (mg C d^{-1})			1169857	24822239	97778778	73700261	-1.028E8
Total NEP (kg C)			-15	31	93	46	-103
		26	24	31	38	46	
Average NEP (kg C d^{-1})	18						

d'Argent	05-May	22-Jul	02-Nov
0 to 1	9.48	7.97	10.11
1 to 2	9.59	7.99	10.07
2 to 3	9.53	7.96	10.08
3 to 4	9.16	7.93	10.04
4 to 5	8.87	6.49	10.01
5 to 6	8.97	2.97	9.97
6 to 7	8.4	1.95	9.96
7 to 8	7.68	1.55	9.91
8 to 9	7.35	1.01	9.93
9 to 10	7.3	1.01	10.01
10 to 11	7.08	0.73	10.02
11 to 12	6.93	0.63	10.02
12 to 13	6.71	0.5	9.97

13 to 14	7	0.37	9.95
Bowker			
Depth	05-May	22-Jul	02-Nov
0 to 1	10.51	8.54	10.48
1 to 2	10.88	8.56	10.47
2 to 3	10.95	8.54	10.48
3 to 4	10.96	8.54	10.46
4 to 5	11.26	8.54	10.47
5 to 6	11.47	8.54	10.47
6 to 7	11.68	8.59	10.5
7 to 8	11.76	9.29	10.51
8 to 9	11.85	11.27	10.57
9 to 10	11.92	11.77	10.59
10 to 11	11.75	12.15	10.65
11 to 12	11.6	12.2	10.67
12 to 13	11.53	12.32	10.73
13 to 14	11.4	12.33	10.75
14 to 15	11.31	12.25	10.81
15 to 16	11.27	12.27	10.82
16 to 17	11.17	12.01	10.87
17 to 18	11.14	12	10.85
18 to 19	11.06	11.73	10.82
19 to 20	10.99	11.69	10.53
20 to 21	10.98	11.61	10.15

Brome			
Depth	06-May	23-Jul	03-Nov
0 to 1	11.24	7.85	10.46
1 to 2	11.35	7.82	10.4
2 to 3	10.63	7.82	10.4
3 to 4	10.54	7.77	10.39
4 to 5	10.48	7.74	10.38
5 to 6	9.95	7.56	10.37
6 to 7	9.34	7.04	10.39
7 to 8	9.03	4	10.42
8 to 9	8.78	0.72	10.46
9 to 10	5.71	0.16	10.49
10 to 11	5.36	0.15	0.56
11 to 12	2.4		

Orford			
Depth	05-May	22-Jul	02-Nov
0 to 1	10.43	8.78	10.49
1 to 2	10.47	8.79	10.45
2 to 3	10.53	8.8	10.45
3 to 4	10.53	8.82	10.45
4 to 5	10.54	8.81	10.47
5 to 6	10.64	8.82	10.43
6 to 7	12.1	12.02	10.42

7 to 8	12.19	13.36	10.43
8 to 9	12.17	13.34	10.43
9 to 10	12.16	13.16	10.44
10 to 11	11.2	12.65	10.43
11 to 12	11.24	12.35	10.46
12 to 13	11.11	12.05	10.51
13 to 14	11.1	11.37	10.53
14 to 15	10.98	11.21	10.52
15 to 16	10.98	11.01	10.48
16 to 17	10.98	10.93	10
17 to 18	10.88	10.78	9.2
18 to 19	10.8	10.22	9.06
19 to 20	10.79	10.22	8.87
20 to 21	10.71	10.22	8.83

Waterloo			
Depth	06-May	23-Jul	03-Nov
0 to 1	10.27	8.18	8.95
1 to 2	10.25	8.21	8.88
2 to 3	9.6	7.83	8.75
3 to 4	8.99	6.23	8.84
4 to 5	7.85	4.8	8.83
5 to 6	2.71		8.67

La Pêche			
Depth	03-Jun	25-Jul	31-Oct
0 to 1	9.86	8.74	8.95
1 to 2	9.67	8.865	8.88
2 to 3	9.75	8.99	8.86
3 to 4	9.83	8.98	8.86
4 to 5	9.71	8.99	8.81
5 to 6	9.47	9	8.81
6 to 7	9.4	8.7	8.76
7 to 8	9.3	4.32	8.81
8 to 9	7.16	0.82	8.88

Phillippe			
Depth	03-Jun	25-Jul	31-Oct
0 to 1	10	8.45	9.44
1 to 2	9.99	8.44	9.4
2 to 3	9.99	8.45	9.4
3 to 4	10.03	8.42	9.38
4 to 5	10.03	8.39	9.38
5 to 6	10.03	8.37	9.38
6 to 7	10	8.56	9.4
7 to 8	9.92	9.23	9.44
8 to 9	9.71	6.63	9.49
9 to 10	9.27	4.71	9.54
10 to 11	8.3	2.93	9.6
11 to 12	8.07	2.06	9.7