

The summer metabolic balance in the epilimnion of southeastern Quebec lakes

Abstract—On the basis of data collected in Quebec lakes, del Giorgio and Peters (1994) and Carignan et al. (2000) have come to opposite conclusions regarding the metabolic balance between heterotrophy and autotrophy in lakes in general. In the present study, epilimnetic oxygen and carbon dioxide saturation was measured in 33 lakes from the St. Lawrence Lowlands region of Quebec to examine the extent of epilimnetic net heterotrophy (i.e., $O_2:CO_2$ balance) in lakes of different characteristics. We found that ~75% of the lakes were undersaturated with oxygen and supersaturated with CO_2 . There was a strong negative relationship between the departures of O_2 and CO_2 from saturation. What has not been noted elsewhere is that oxygen concentrations were negatively related to dissolved organic carbon (DOC) concentration, and, therefore, metabolic gas balances could be predicted from DOC; a value between 4 and 6 mg L⁻¹ DOC corresponds to metabolic equilibrium. Because most of the lakes in del Giorgio and Peters (1994) had DOC concentrations above this threshold and most lakes in Carignan et al. (2000) were below, their apparently contradictory conclusions can be reconciled within a larger general theory. Contrary to studies elsewhere, however, we found that the degree of oxygen undersaturation increased with lake trophic status, expressed either as total phosphorus or nitrogen concentrations.

Over the past few years, fundamental questions have been raised in both marine and freshwaters regarding the role of allochthonous carbon loads to the ecosystem's overall metabolism (e.g., del Giorgio and Peters 1993; Cole et al. 1994, 2000; del Giorgio et al. 1997; Duarte and Agusti 1998; Williams and Bowers 1999). The recent article of Carignan et al. (2000) on the balance between epilimnetic primary production and respiration in 12 oligotrophic lakes brought new data to the debate on net lake ecosystem metabolism and, by directly contradicting earlier claims, has deepened the controversy. In their detailed study of 12 Laurentian Shield lakes, Carignan et al. (2000) found that even in the most oligotrophic lakes, where net heterotrophy is believed to be most likely (del Giorgio and Peters 1994; del Giorgio et al. 1997; Duarte and Agusti 1998), gross photosynthesis nearly always exceeded planktonic respiration. The implication is that allochthonous sources of organic carbon play a relatively minor role in the lake carbon cycle, a view clearly at odds with the current view of lakes, in which allochthonous carbon is believed to fuel a large part of bacterial metabolism (e.g., Tranvik 1992).

The apparent contradiction between the results of Carignan et al. (2000) and del Giorgio and Peters (1994) was all the more inescapable, given that the opposing views were based on sets of lakes that are located within 200 km of one another. However, although they share many common attributes, these regions are very different geologically, topographically, and therefore limnologically. Although Carignan et al.'s lakes are all located on the Precambrian shield, those of del Giorgio and Peters are all located off the shield, in the Eastern Townships region of Quebec, which is underlain

by the sedimentary geology of the St. Lawrence Lowlands and characterized by elevated pH and alkalinities. It is an oversight that these and other differences have not been considered important enough to influence the metabolic balance of lakes. Instead, the incongruity between their respective conclusions was attributed to differences in methodology and also to possible misinterpretation of ¹⁴C-based primary production measurements (Carignan et al. 2000).

In the present article, we present evidence based on observed O_2 profiles and calculated CO_2 values from an independent data set of 33 lakes from the Eastern Townships region of Quebec. Although the concentrations of both carbon dioxide and oxygen primarily reflect the biotic metabolic balance of the epilimnion, they are also affected by abiotic processes such as the photolytic production of CO_2 or groundwater inputs. Therefore, the term "net metabolic balance" used throughout this paper represents the sum of both biotic and abiotic processes influencing gas concentrations. Our results suggest that the apparently contradictory generalizations reached by del Giorgio and Peters (1994) and Carignan et al. (2000) may both be correct within their proper frames of reference: our inferred net balance of epilimnetic metabolism (as calculated on the basis of departures from saturation concentrations) differed consistently between regions. We suggest that these regional differences are the result of the lower concentrations and possibly the more refractory nature of the dissolved organic carbon (DOC) in oligotrophic shield lakes than in lowland lakes: ecosystem metabolic balance over all regions varies continuously and linearly along the gradient of DOC concentration.

Study sites—We sampled 33 lakes from the Eastern Townships region ~100 km east of Montreal an average of four times during the summer of 1999. The region is underlain by a sedimentary geology and surface deposits consists mostly of alternating thick and thin glacial till and some glacio-lacustrine fine sediments. In addition to oxygen and temperature profiles, integrated epilimnetic samples were analyzed for standard chemistry. Total phosphorus (TP) and total dissolved phosphorus were measured after persulfate digestion and autoclaving of unfiltered and filtered (0.45 μ m cellulose acetate syringe filters) samples. Total nitrogen (TN) and total dissolved nitrogen were measured as nitrates after alkaline persulfate digestion. Nitrate concentrations were measured after reduction through a cadmium coil. DOC concentrations of filtered water samples (0.45 μ m surfactant-free membrane filters) were measured on a Shimadzu TOC analyser after acidification and N_2 sparging.

O_2 and CO_2 gas concentrations—All oxygen profiles were obtained with a Wissenschaftlich-Technische Werkstätten oxygen meter calibrated in the field in a humid chamber. The profiles were used to calculate the epilimnetic oxygen concentration (average of epilimnetic 1-m interval profiles val-

Table 1. Mean chemical characteristics of the lakes sampled in this study.

Lake	Lake area (km ²)	DOC (mg L ⁻¹)	Total N (μg L ⁻¹)	DON (μg L ⁻¹)	Total P (μg L ⁻¹)	Chl <i>a</i> (μg L ⁻¹)	Alkalinity (μeq L ⁻¹)	pH from mean [H ⁺]	[O ₂] difference from saturation (μM)	[CO ₂] difference from saturation (μM)
Aylmer	32.38	10.0	602.1	411.0	16.9	3.3	478.8	7.50	-31.6	18.96
Bisby	0.22	11.2	565.3	455.5	22.5	6.6		7.36	-43.7	
Bowker	2.45	3.8	173.3	84.4	5.1	2.3	234.5	7.15	3.1	19.23
Brompton	11.71	6.2	304.2	208.5	5.3	3.0	342.6	7.70	4.5	1.29
Denison	0.31	5.2	565.0	409.4	34.8	7.9	791.2	7.63	-28.6	29.96
Drolet	2.79	4.0	460.8	341.7	14.0	5.8	300.2	7.69	-11.0	-0.34
Elgin	3.71	7.3	438.6	215.6	8.0	3.7	366.8	7.58	-13.2	7.32
Est	0.78	6.1	451.7	372.8	10.7	4.0	501.5	7.76	-22.2	5.52
Fraser	1.62	4.6	299.3	202.7	9.6	2.6	351.0	7.83	7.7	-1.69
Huit	2.38	9.4	467.9	414.2	12.8	4.0	445.7	7.50	-44.2	16.59
Leclerc	0.06	4.5	331.6	198.0	15.8	10.3	454.4	7.45	-7.0	20.87
Libby	0.43	4.2	296.3	229.1	12.9	51.	460.5	7.65	-14.3	9.22
Lovering	4.89	7.0	366.8	299.3	11.5	2.8	485.9	7.89	-2.8	0.36
Lyster	1.88	3.5	232.1	146.7	5.0	1.6	542.6	7.86	0.1	2.81
Magog	11.48	3.8	354.1	266.7	16.0	3.2	954.5	8.20	-17.4	-6.2
Malaga	0.23	5.7	257.7	223.5	6.7	3.8	265.8	7.60	-19.3	-3.5
Massawippi	18.71	4.4	514.1	163.0	8.4	4.3	1,620.9	8.63	2.6	-4.65
Miroir	0.64	6.0	471.9	221.1	9.2	4.1	613.4	7.72	-20.0	12.19
Montjoie	3.26	5.7	278.7	224.5	8.2	2.4	283.3	7.45	1.5	7.93
Mégantic	27.86	5.2	426.5	206.0	6.4	2.9	293.4	7.44	-10.5	8.65
O'Malley	0.17	3.9	297.7	252.3	9.6	2.3	861.9	8.19	-8.1	-0.61
Parker	0.23	9.1	517.2	431.1	18.1	4.4	631.8	7.56	-29.6	24.2
Petit Brompton	0.71	4.7	278.4	212.2	6.1	2.7	749.1	7.80	-0.2	12.96
Saint-Georges	0.51	8.1	630.1	428.2	31.8	16.5	616.1	8.29	-9.9	-6.28
Silver	0.71	4.7	330.9	199.6	8.4	3.8	890.8	8.18	-4.6	-0.35
Simoneau	0.45	4.1	246.4	158.6	6.5	2.4	351.5	7.55	-9.8	7.8
Stoke	0.38	5.6	570.2	378.1	16.8	12.0	783.2	8.68	6.7	-9.91
Stukely	4.01	4.5	238.7	178.5	6.2	2.0	426.8	7.87	10.9	-0.54
Tomcod	0.81	8.0	1,043.3	558.1	104.5	52.5	1,071.9	8.71	-15.1	-8.9
Trois Lacs	2.40	8.3	567.5	428.1	25.1	7.0	938.4	7.79	-21.6	20.28
TruiteA	2.40	8.9	436.8	290.5	7.8	1.7	369.9	7.27	-37.5	27.31
TruiteO	0.35	6.6	299.0	230.1	7.6	2.9	559.5	7.68	-14.7	12.13
Webster	0.06	5.2	420.5	301.8	16.1	3.1	521.5	9.83	18.7	-13.26

ues) and were expressed as a concentration differential (μM) from elevation and temperature corrected saturation values. The top of the thermocline was defined as the depth where the epilimnetic temperature gradient first exceeded 1°C m⁻¹.

CO₂ concentrations were obtained from pH and alkalinity measurements (Gran titration) following the method of Stumm and Morgan (1981), after correction for ionic strength (Cole et al. 1994). Carbon dioxide concentrations were also expressed as a differential from temperature and elevation corrected saturation values assuming an atmospheric CO₂ value of 370 μatm. The pH and alkalinity measurements were done on integrated epilimnetic samples.

Although temporal variability in dissolved gas concentrations within lakes existed, it was a relatively minor component of the total variation. Over 80% of the variability in both O₂ and calculated CO₂ concentration was attributable to among lake differences, and we therefore felt justified in using summer averages for all variables. A complete data table is provided in Table 1. Nevertheless, weighted regression was used in analyses with O₂ departure from saturation

concentration as the dependent variable, where the weights were the reciprocal of the temporal variance.

Results and discussion: lake chemistry—The basic physical and chemical characteristics of the 33 lakes are given in Table 1. The lakes vary widely, from shallow to deep, oligotrophic to eutrophic (TP 5–105 μg L⁻¹), and DOC poor to intermediate (3–11 mg L⁻¹). They are generally well-buffered (alkalinity >250 μeq L⁻¹), with slightly to very alkaline pH values (pH > 7). According to their TN:TP ratios, all lakes are phosphorus limited (mean = 81 mole:mole, range = 22–150).

Balance between O₂ undersaturation and CO₂ supersaturation—Epilimnetic O₂ and CO₂ concentrations varied moderately among our lakes, between 221 and 275 μM for oxygen and between 3 and 40 μM for CO₂. These values show that 75% of our lakes are undersaturated with oxygen and also oversaturated with CO₂, which suggests persistent epilimnetic net heterotrophy in these lakes, a conclusion

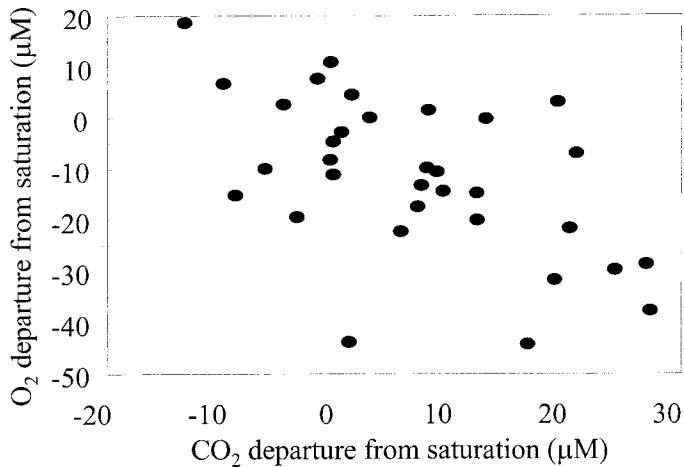


Fig. 1. Relationship between O_2 and CO_2 departure from saturation (μM) in 33 lakes from the Eastern Township region.

very similar to that of del Giorgio and Peters (1994) for lakes of the same region. These carbon dioxide concentrations fall in the low range of other Canadian, mostly shield, lakes (Hesslein et al. 1990). Despite these narrow ranges, Fig. 1 illustrates the highly significant relationship between O_2 and CO_2 concentrations, expressed here as a differential from saturation ($r^2 = 0.41$, $P < 0.01$). Although it is an imperfect relationship, its major axis parameters (more appropriate here than ordinary least-squares calculations, given comparable measurement errors in the two variables; Prairie et al. 1995) suggest that the two reflect the metabolic balance: the intercept is not significantly different from 0 ($P > 0.05$) (i.e., lakes at saturation with oxygen are also at saturation with respect to CO_2) and the slope is -0.96 , consistent with an average respiratory quotient ($O_2:CO_2$) near 1.

Part of the noise in this relationship is probably due to factors other than respiration that influence CO_2 concentration. In particular, small amounts of groundwater highly elevated in CO_2 can readily alter the lake's concentration. Although we did not measure the groundwater contribution to the hydrological budget of these lakes, we examined this hypothesis indirectly by testing whether the residuals from the CO_2 vs O_2 relationship (Fig. 1) were correlated with topographical factors believed to be surrogates of groundwater importance. We found that watershed slope showed a highly significant positive correlation with the residuals of the $\Delta CO_2 - \Delta O_2$ relationship ($r^2 = 0.23$, $P < 0.01$). This is consistent with theory to the extent that the relative contribution of groundwaters to the total hydrological budget of a lake is expected to be greater in catchments with high relief. Because of the confounding influence of factors other than lake metabolism on CO_2 departures from saturation, the subsequent analyses focused on O_2 departure from saturation as a more conservative measure of lake metabolism, because CO_2 supersaturation can be much greater than oxygen undersaturation in groundwaters.

Relationship between O_2 undersaturation and DOC—A systematic epilimnetic oxygen undersaturation implies that the rate of oxygen consumption by respiration and photo-

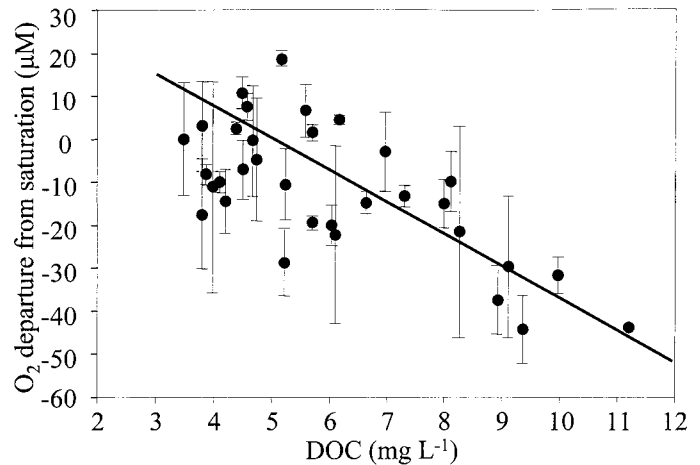


Fig. 2. Relationship between O_2 departure from saturation (μM) and DOC ($mg L^{-1}$) concentration in our 33 lakes. Error bars represent ± 1 SD. Solid line is the weighted regression equation.

chemical oxidation exceeds the rate of oxygen supply from primary production and atmospheric invasion. Similarly, systematic CO_2 supersaturation implies that the rate of CO_2 supply from stream flow, respiration, and photo-oxidation exceeds the rate of consumption by photosynthesis. The very clear negative relationship between oxygen undersaturation and DOC concentration ($r^2 = 0.45$, $P < 0.0001$, Fig. 2) within the region certainly suggests that allochthonous DOC plays an important role in the lakes' metabolism. Although the photolysis of DOC would also consume oxygen and could therefore also explain this inverse relationship, photolytic degradation should be relatively unimportant in these circumneutral to alkaline lakes (Gennings et al. 2001). In our lakes, the higher the DOC concentration, the more undersaturated the oxygen concentration is. A similar relationship was obtained with dissolved organic nitrogen (DON; $r^2 = 0.36$, $P < .001$). When we included DON:DOC as a measure of the quality of the DOC in a multiple regression with DOC, both variables explained significant portions of the variation in the oxygen departure from saturation concentration ($r^2 = 0.65$, $P < 0.001$). More labile dissolved organic matter (high DON:DOC) is associated with greater undersaturation than would be predicted on the basis of DOC concentration alone. This largely explains the wider scatter at the low DOC end (Fig. 2). However, because DON values are rarely available in other regions, we restricted further analysis to the O_2 -DOC relationship alone.

Contrary to the findings of del Giorgio and Peters (1994), we found a negative relationship between O_2 departure from saturation and lake trophic status, expressed as either phosphorus or nitrogen (circles in Fig. 3). Although not as good a predictor of O_2 undersaturation as either DOC or DON, these relationships cast doubts on the general claim that the net heterotrophy is to be found mostly in oligotrophic lakes (Duarte and Agusti 1998). In addition, even though del Giorgio and Peters (1994) concluded that net heterotrophy is more likely in oligotrophic systems, their own relationships are ambiguous with respect to the role of lake trophic because they depend critically on how the balance between produc-

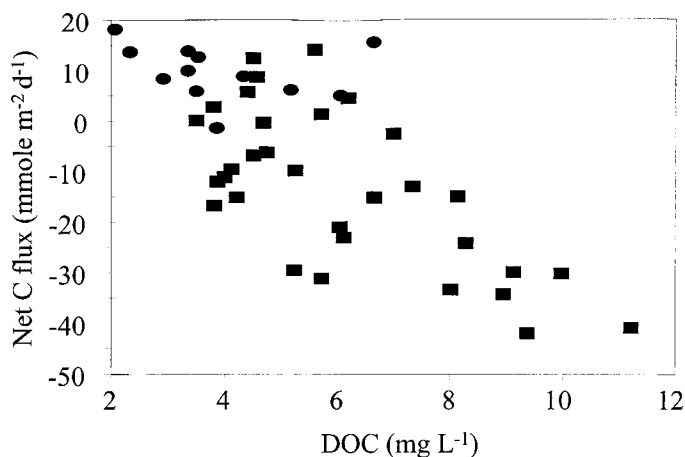


Fig. 4. Relationship between net flux of carbon ($\text{mmole m}^{-2} \text{d}^{-1}$) and DOC. Circles are data from Carignan et al. (2000), and squares are from the present study. Negative values correspond to net evasion. One outlier with a very large net flux value ($154 \text{ mmole m}^{-2} \text{d}^{-1}$, Lac Webster) due to the high chemical enhancement value at high pH was omitted from this graph.

tion and respiration is expressed. As a P:R ratio, net heterotrophy is apparently increasingly favored in oligotrophic systems (fig. 3 in del Giorgio and Peters 1994). However, when expressed as a net absolute rate (production – respiration), it may not be. For instance, the regression equations given in del Giorgio and Peters (1994) to predict respiration or production as a function of phosphorus (the first two equations in their table 2 and fig. 2b) can be combined to estimate net metabolic balance by subtraction. The resulting calculations show that net metabolism is not monotonically related to lake trophicity at all! Instead, their equations predict that it should be negatively related to phosphorus in oligo- to mesotrophic lakes and positively related in eutrophic lakes (solid line in Fig. 3). Cole et al. (2000) also provide evidence that net metabolic balance and nutrient status are not necessarily closely coupled. Given that $\sim 80\%$ of our lakes are in the oligo-mesotrophic range and that our measure of net metabolism (oxygen departure from saturation concentration) is clearly more closely related to an absolute rate difference than a dimensionless relative P:R ratio, our negative trend between oxygen undersaturation and lake trophicity is actually consistent with their original results. In our view, however, expressing net metabolic balance as a P:R ratio can be misleading. In their net heterotrophic lakes, there is no significant relationship between P:R ratios and the measured net balance (production – respiration) ($r^2 = 0.08$, $P > 0.25$). Net balance is quantitatively most meaningful.

Under the assumption of average wind speeds of $\sim 3 \text{ m s}^{-1}$ (Environment Canada), a respiratory quotient of 0.96 (obtained from Fig. 1), our oxygen concentration values can be converted to areal carbon fluxes following the calculations of Cole and Caraco (1998). These ranged from roughly -45 (efflux) to $+18$ (influx) $\text{mmoles C m}^{-2} \text{d}^{-1}$. The linear relationship between oxygen undersaturation and DOC concentration suggests that the rate of removal follows a first-order reaction process. Relative to the DOC stocks, the effluxes correspond to an average mass transfer coefficient of

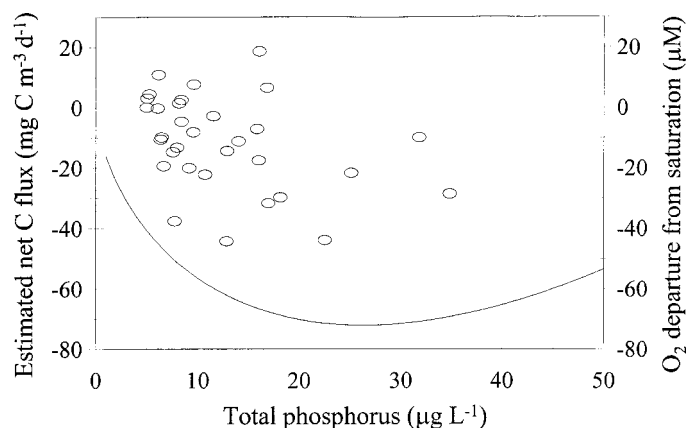


Fig. 3. Solid line corresponds to implicit relationship between net metabolism ($\text{mg C m}^{-3} \text{d}^{-1}$) and phosphorus concentration derived from the empirical equations of del Giorgio and Peters (1994). Circles are the oxygen departure from saturation (μM) as a function of total phosphorus from this study. The numerical correspondence between the two vertical axes is fortuitous.

25 mm d^{-1} ($\text{SD} \pm 16$, $\text{SE} \pm 3 \text{ mm d}^{-1}$) or, with the assumption that these fluxes occur essentially during the warm months (140 d), 3.5 m yr^{-1} . This value is close to the average measured DOC mass-transfer coefficient (ν) of 3.2 m yr^{-1} derived from mass balance in Ontario shield lakes (Dillon and Molot 1997). This correspondence between effluxes and ν also suggests that carbon loss as estimated from mass balance is mostly in the form of CO_2 evasion and not sedimentation (Molot and Dillon 1996). This is at odds with the view that carbon loss is mostly in the form of sedimentation in high-alkalinity lakes (Dillon and Molot 1997). This discrepancy may reflect regional differences but may also be attributed to the wide variability in mass transfer coefficient among lakes.

According to the regression equation of the relationship illustrated in Fig. 2, the DOC concentration at which oxygen is, on average, at saturation is $\sim 5 \text{ mg L}^{-1}$ DOC. Note that this threshold value has significant scatter and may be better represented as a threshold region of $4\text{--}6 \text{ mg L}^{-1}$ DOC. At higher DOC concentrations, lakes (i.e., their epilimnia) are expected to be net heterotrophic. Nevertheless, the average threshold value of 5 mg L^{-1} DOC is nearly identical to that found by Hope et al. (1994) in relation to pCO_2 departure from atmospheric equilibrium. Interestingly, 9 out of the 12 lakes studied by Carignan et al. (2000) were below this threshold value, whereas 75% of the lakes in del Giorgio and Peters (1994) were above. In light of this difference, it comes as no surprise that their general conclusions regarding the prevalence of epilimnetic net heterotrophy differed so markedly.

This general trend between the net metabolic balance and DOC holds equally well for the lakes of Carignan et al. (2000). Computed average areal net metabolic balance (gross primary production – community respiration) from their data table shows a clear and significant relationship with DOC, except for Lac à l'Ours. The only difference in this relationship is that it crosses the zero line at $\sim 6.5 \text{ mg L}^{-1}$ DOC, a value slightly higher than that for the Townships

region. Combining the data from Carignan et al. (2000) and our own, expressed as an areal carbon flux calculated above, shows that the lakes from the two regions appear to follow the same relationship between net metabolism and DOC (Fig. 4). This clearly shows that the general conclusions reached about net metabolism in lakes of these two regions are not in any way contradictory; they are different end members of a single continuum. The fact that the data from both regions follow basically the same relationship (Fig. 4) strongly suggests that arguments about differences in methodology, and in particular about the meaning of ^{14}C -based production estimates, were likely ill-founded. Net heterotrophic balance is simply not expected in lakes with such low DOC.

In spite of the clear compatibility of the data of Carignan et al. (2000) with our own, the two studies are not strictly commensurable. For instance, their net metabolic balance was derived from laboratory incubations of epilimnetic waters and therefore only includes the pelagic component. Our measures of net metabolism (CO_2 and O_2 concentration departure from equilibrium) also include the production and respiration components of epilimnetic sediments. In our lakes, the proportion of the lake sediment surface area that is located within the epilimnion varies widely, from 19% to 100%. However, we found that this variable did not enter as an additional independent variable in models that predict oxygen undersaturation. This suggests that epilimnetic sediments probably constitute a small component of the total epilimnetic metabolism, maybe because the supply of organic material to the sediments is known to be smaller in shallow areas (Carignan and Lean 1991). However, the proportion of very shallow lakes in our data set was small, so our ability to detect a significant effect was probably insufficient.

The difference in DOC concentrations between shield and off-shield lakes in Quebec appears to be a general regional phenomenon. In our lakes, DOC concentrations varied negatively with watershed slope, and this is true also of shield lakes (Rasmussen et al. 1989; D'Arcy and Carignan 1997). However, the average watershed slope is nearly twice as steep for shield lakes as it is in the Townships (Laurentian Shield, 8.8° and Townships, 4.8° ; Laurentian Shield lakes data, R. Carignan pers. comm.).

There is also some evidence that not only does the concentration of DOC differ significantly between the two regions, but so does its nature. In particular, the color of the DOC is quite different, a characteristic usually linked to the aromaticity of the DOC and perhaps to its recalcitrance. As a general comparative measure of color, the contribution of the DOC to the light extinction coefficient was estimated to be $\sim 0.19 \text{ m}^{-1} (\text{mg L}^{-1})^{-1}$ DOC in the Laurentian lakes but only $\sim 0.07 \text{ m}^{-1} (\text{mg L}^{-1})^{-1}$ DOC in the Townships. It is not clear whether this difference in the DOC color is due to the intrinsic difference in the nature or origin of the DOC or whether it is related to the more rapid photobleaching in lakes with higher pH and alkalinity such as in the Townships (Reche et al. 1999). Regardless of this color difference however, Fig. 4 suggests that degradation is equivalent in the two regions.

In conclusion, independent data based on oxygen and cal-

culated carbon dioxide concentrations from 33 lakes suggest that the net lake metabolism should be viewed along a DOC gradient, not a lake trophic gradient. According to our model, lakes are expected to be net autotrophic when DOC concentrations are $< 5 \text{ mg L}^{-1}$ and net heterotrophic at higher concentrations. The incompatible conclusions of Carignan et al. (2000) and del Giorgio and Peters (1994) regarding the prevalence of net heterotrophy in lakes can thereby be reconciled by consideration of regional DOC characteristics.

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Effects of groundwater flux on open-channel estimates of stream metabolism

Abstract—The open-channel oxygen method can produce precise estimates of photosynthesis (P) and respiration (R) over a wide range of stream conditions. It is widely recognized that flux of groundwater contributes to the oxygen mass balance for a stream. However, groundwater flux is rarely considered in open-channel estimates of stream metabolism, and no guidelines have been established regarding the conditions under which it can be ignored. The purpose of this paper is to describe a method for predicting the effect of groundwater flux on estimates of metabolism and thereby establish the conditions under which flux of groundwater can lead to large errors in estimates of metabolism. Estimation of P is not significantly affected by flux of groundwater. Ecosystem R , however, can be greatly overestimated where the oxygen concentration of groundwater is substantially lower than the concentration in the channel. Although the effects of groundwater flux on estimates of metabolism often are trivial, rates of flux can be sufficiently high in many streams, at least during some part of the year, to affect estimates of R where the oxygen concentration differs substantially between groundwater and surface water. Thus, the potential contribution of groundwater flux to oxygen mass balance should always be evaluated when the open-channel method is used.

The open-channel oxygen method can provide precise, system-level estimates of ecosystem metabolism over a wide range of stream conditions (McCutchan et al. 1998). The open-channel method also incorporates respiration in deep sediments, which often accounts for a large fraction of total respiration in streams and may be underestimated by chamber techniques (Grimm and Fisher 1984; Fellows et al. 2001). Application of the open-channel method has become

common since the advent of recording field oxygen meters and improvements to methods for measuring reaeration (exchange of oxygen with the atmosphere). Assumptions that are implicit in open-channel estimates of metabolism have come under scrutiny, however, as investigators have begun to test the limitations of the method.

Open-channel estimates of photosynthesis (P) and respiration (R) can be based on calculation of mass balance for carbon dioxide but most commonly are based on mass balance for dissolved oxygen. Changes in oxygen concentration of a stream over time or distance reflect the balance of metabolic processes (P and R) and reaeration. Flux of groundwater also must be considered in streams where the effect of groundwater on oxygen mass balance is large relative to rates of biological processes and reaeration, or metabolism will be estimated with error. Odum (1956) considered the potential effects of groundwater flux on the mass balance of oxygen in streams, and more recent work (Choi et al. 1998; Jones and Mulholland 1998) has demonstrated empirically that flux of groundwater can greatly affect gas concentrations in streams, but the effects of flux on estimates of stream metabolism have not been examined explicitly. Although practitioners of the open-channel method (e.g., Marzolf et al. 1994; Uehlinger and Naegeli 1998; Fellows et al. 2001) often have attempted to confine their work to reaches where rates of groundwater flux are low, the potential for error in open-channel estimates of metabolism has not been studied. The purpose of this paper is to establish the conditions under which flux of groundwater can lead to bias in estimates of metabolism and to describe a method for minimizing such errors.