Organic matter mineralization in lake sediments: A within and among lake study.

by

Cornelia E. den Heyer

Department of Biology
McGill University
Montreal, Quebec
Canada

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Thesis Abstract

Organic matter mineralization by sediment bacteria was measured by the accumulation of DIC + CH_4 in the water overlying intact cores taken from littoral and profundal sediments of 9 lakes. The variability in areal carbon mineralization was much greater within lakes than among lakes, with the rate of organic matter mineralization in littoral sediments, on average, 3 fold higher than in the deeper sediments.

Sixty per cent of the variation in summer carbon mineralization rates is explained by site depth, a surrogate variable which incorporates the effect of temperature and may also be reflecting organic matter quality and/or supply. Lake-specific variables become useful predictors of carbon mineralization only after the site depth is considered. Those lake-specific characteristics most strongly correlated to residuals of the regression with depth are the catchment area to lake area ratio (CA:LA) and the water residence time. In lakes with a larger CA:LA and a shorter water residence time organic matter mineralization in the sediments at a given depth is less. These two variables are interchangeable and appear to be acting as surrogates for the amount and/or quality of organic matter being supplied to the sediments. The rate of organic matter mineralization in the sediments is independent of the algal biomass in the mixed layer and the two measures of relative input of autochthonous material to the sediment, the C:N and $\delta^{13}C$ ratios of organic matter in the top centimeter. The variation in total mineralization and the mean areal mineralization among lakes is primarily a function of lake morphometry. Total organic matter mineralization in sediments is greater in larger lakes but the rate per unit area is less, reflecting the decrease in relative importance of the littoral zone.

A comparison of the mineralization in sediments overlain by epilimnetic water to the whole lake sediment mineralization demonstrates the overwhelming importance of the littoral sediments in organic matter mineralization, with more than half (54-100%) of the

mineralization in the sediments occurring in the littoral zone. However, the littoral sediments account for less than 20% of the gross respiration in the epilimnion. Epilimnetic waters, which support a large plankton biomass, have 4 to 5 fold higher rates of oxygen consumption per unit volume than hypolimnetic water. Thus, the importance of the sediments in whole lake metabolism is a function of both the trophy and morphometry of lakes.

Résumé

Le taux de minéralisation de la matière organique a été estimé par l'accumulation du DIC + CH_4 dans l'eau interstitielle de carottes non-pertubées receuillies dans les sédiments des zones littorales et profondes de 9 lacs du Québec. La variabilité intra-lac dans le taux de minéralisation du C par unité de surface était supérieure à la variabilité inter-lac. Cette dernière est l'effet d'un taux de minéralisation 3 fois plus élevés dans les sédiments de la zone littorale par rapport à la zone profonde d'un même lac.

Soixante pourcent de la variabilité de la moyenne estivale du taux de minéralisation était expliqué par la profondeur du site, étant donné que ce dernier réflète l'effet de la température et la qualité et/ou la quantité de matière organique. Après avoir considéré la profondeur du site, certaines variables morphométriques du lac deviennent utiles pour prédire la minéralisation du C des sédiments. Le ratio de l'aire du bassin versant versus l'aire du lac (CA:LA) et le temps de résidence d'un lac étaient fortement corrélés avec l'erreur résiduelle de la relation entre la minéralisation et la profondeur du site. Dans les lacs avec un grand CA:LA et un court temps de résidence, le taux de minéralisation de la matière organique dans les sédiments était plus faible pour une même profondeur. Ce taux de minéralisation était indépendant de la biomasse phytoplanctonique dans la colonne d'eau et l'apport en matière autochtone. Ce dernier a été estimé en déterminant les ratios de C:N et le $\delta^{13}C$ de la matière organique dans le premier centimètre des sédiments. Il semble que la variation dans la minéralisation totale et la minéralisation moyenne par unité de surface dans les sédiments soit une fonction de la morphométrie du lac. Le taux de minéralisation dans les sédiments est plus élevé dans un grand lac, mais ce taux par unité de surface est plus faible, ce qui réflète une diminution dans l'importance relative de la zone littorale.

Le pourcentage de minéralisation qui s'effectue dans les sédiments sous-jacente de l'eau de l'épilimnion est plus que la moité (54-100%) de la minéralisation des sédiments du

lac entier, démontrant l'importance significative de l'activité bactérienne dans les sédiments de la zone littorale. Cependant, les sédiments de la zone littorale représentent moins de 20% de la respiration brute dans l'épilimnion par la biomasse planctonique de l'épilimnion consomme 4 à 5 fois plus d'oxygène par unité de volume que dans l'hypolimnion. L'importance des sédiments dans le métabolisme d'un lac entier est une fonction du niveau trophique du lac et de ses charactéristiques morphométriques.

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Preface

The Faculty of Graduate Studies and Research of McGill University requires that the following text be reproduced in full in the preface.

> Candidates have the option of including, as part of the thesis, the text of a paper submitted or to be submitted for publication, or the clearly-duplicated text of a published paper. These texts must be bound as an integral part of the thesis.
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This thesis is written in manuscript style. I collected the samples with the help of a number of friends and technicians. I performed the laboratory and statistical analysis

reported in the thesis. I also wrote the manuscript and will be submitting version of chapter 1 for publication in Limnology and Oceanography. My supervisor, and co-author, Dr. Jacob Kalff assisted me throughout the project and provided invaluable criticism and discussion of the manuscript. Roxane Maranger kindly translated the abstract.

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'SHHH. Don't disturb the cores.'

General Introduction

Bacteria are the major decomposers of organic matter in aquatic systems (Fenchel and Blackburn 1979). Through consumption of oxidants and release of reduced products they can have dramatic effects on the chemistry and biota of lakes. For example, depletion of dissolved oxygen (O_2) in hypolimnetic waters enhances phosphorus release from sediments (review see Boström et al. 1982) and can result in summer and winter fish kills, while anaerobic respiration in the sediments generates alkalinity (Kelly et al. 1982; Kelly and Rudd 1984; Kelly et al. 1987). Recent work in the water column has also shown bacteria to be an important link between dissolved organic matter and the rest of the biota (Sherr and Sherr 1988, 1991; Christofferson et al. 1990; Pace et al. 1990). However, in the sediments there is less grazing on bacteria than in the water column (Kemp 1990). Therefore, the most important role of the bacteria in the sediments is the mineralization of organic matter.

The sediments may be the primary site for organic matter decomposition in shallow aquatic systems, such as lakes, where the sediment area to lake volume ratio is high. Bacteria are two to three orders of magnitude more abundant per unit volume in the sediment than in the water column above (Duarte et al. 1988; Schallenberg et al. 1989; Schallenberg and Kalff 1993), and although as few as 5 % of the bacteria in the sediment may be active (Dufour and Colon 1992; Butorin 1989), as much as 85 % of O_2 consumption measured in hypolimnia of lakes is attributable to the sediment (Cornett and Rigler 1987).

Research on heterotrophic activity in aquatic systems has traditionally focused on O_2 consumption (Thienmann 1926; Strøm 1931; Hutchinson 1938; Charlton 1980; Hargrave 1973, 1979; Cornett and Rigler 1980, 1987). Consumption of oxygen in

hypolimnetic water was first identified in 1886 by Hoppe-Seyler (see Hutchinson 1957), but the first major advance in predicting the rate of oxygen consumption in hypolimnetic waters and sediments was made by Thienmann (1926), who argued that the hypolimnetic O_2 consumption would depend on both the morphometry of the basin and the planktonic primary production. Strøm (1931) and Hutchinson (1938) devised trophic classification schemes based on the areal hypolimnetic oxygen depletion rates (AHOD), instead of oxygen consumption per unit volume, to eliminate the bias introduced by variability in the thickness of hypolimnia among lakes. Hargrave (1973, 1979) argued that the amount of substrate available to the sediment microbial community was a function of the primary production exported from the surface water and the exposure of that organic material to degradation in the water column. He showed that sediment oxygen consumption (SOC), in both marine and freshwater systems, could be predicted from the ratio of primary production to mixing depth.

More recent predictive models fail to identify the algal biomass in the surface water as an important predictor of AHOD (Charlton 1980; Cornett and Rigler 1987) and SOC alone, is not significantly correlated with primary production (Hargrave 1979). Instead hypolimnetic oxygen consumption appears to be primarily a function of lake morphometry. Both Cornett and Rigler (1980) and Charlton (1980) observed higher rates of AHOD in lakes with thicker hypolimnia. Charlton (1980) suggested that, as SOC was fairly constant (Graneli 1978), the higher AHOD of deeper lakes was the result of increased respiration in the water column. His conceptual model points to a decreasing importance of the sediments in the decomposition and storage of organic matter in thicker hypolimnia (Fig. 1). Indeed, Cornett and Rigler (1987) demonstrated a negative correlation between hypolimnetic thickness and SOC, calculated as the difference between AHOD and oxygen consumption in the water column.

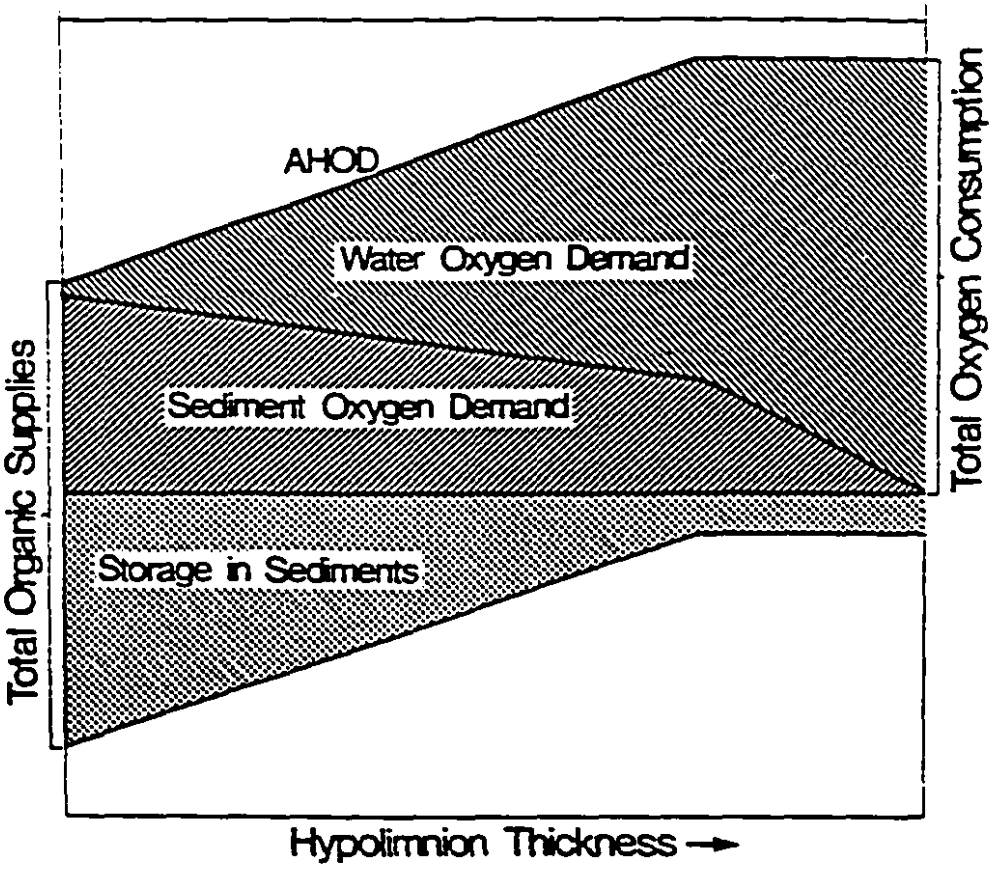
Although the investigations of oxygen consumption provide a good structural framework for further research of organic matter mineralization, the inferences that can be drawn to carbon cycling are limited because aerobic respiration is only one, albeit the most efficient, of several metabolic pathways employed by bacteria. Ohle (1956) suggested the use of carbon dioxide (CO_2) accumulation as an indicator of the bioactivity of aquatic systems in order to circumvent the limitations associated with anaerobic mineralization of organic matter. Carbon dioxide is the end product of both aerobic and anaerobic respiration and, together with methane (CH_4), is also an end product of fermentation. Rich and Devol (1978) found accumulation of dissolved inorganic carbon (DIC) to exceed O_2 consumption in the hypolimnia in 4 of their 5 lakes, and Kelly et al. (1988) showed that the accumulation of DIC plus CH_4 exceeds the consumption of O_2 in the hypolimnetic waters of 3 Ontario lakes, with between 78 and 97% of the organic matter decomposition being associated with anaerobic processes. However, few studies have examined the production (Ramlal et al. 1993; Sweerts et al. 1986; Schallenberg 1992) or the flux (Carignan and Lean 1991) of DIC and CH_4 from lake sediments, and the processes which determine the rate of organic matter mineralization in the sediments remain unresolved.

Microbial ecologists have worked almost exclusively on profundal sediments, even though the majority of lakes are small and effectively dominated by the littoral zone, both in terms of area and primary production (Wetzel 1990). The historical focus on the pelagic zone and the underlying sediments as the more biologically interesting zone of lakes was reinforced by the influential work of Jones and Simon (1981). They found bacteria to be less abundant and less active per gram of dry sediment in littoral than profundal sediments. However, when the variables are more appropriately expressed per unit area or volume, bacteria are both more abundant (Duarte et al. 1988; Schallenberg et al. 1989; Schallenberg and Kalff 1993) and more productive (Sander and Kalff 1993) in shallow than profundal sediments.

The aim of the thesis is to quantify and predict the rates of organic matter mineralization in littoral and profundal sediments of lakes. A multilake sampling regime was used to investigate the importance of lake trophic status and morphometry in predicting areal rates of sediment organic matter mineralization. In chapter 1, I show that areal organic matter mineralization rates are more variable within than among lakes varying considerably in trophy. I present a predictive model for sediment DIC + CH_4 release based on site depth and the ratio of lake catchment area to lake area. Using this model I then estimate the total organic matter mineralization in the sediments for 8 of the study lakes. A comparison of mineralization in the sediments with the mineralization in the sediments overlain by epilimnetic water shows the overwhelming importance of the littoral sediments in sediment organic matter mineralization.

The higher observed rates of organic matter mineralization in the littoral sediments are at least in part due to the higher temperature of the overlying water, but the quality and quantity of organic matter may also be limiting the sediment microbial community. Carbon to nitrogen (C:N) and stable carbon isotope ($\delta^{13}C$) ratios of the organic matter in the surface sediment were measured in an attempt to determine the relative contribution of autochthonous detritus to the substrate of the sediment microbial community. The utility of these two measures of the autochthonous nature of the sediment organic matter is explored in chapter 2. Neither of these measures nor the algal biomass of the surface water is related to the rate of organic matter mineralization in the sediments. However, algal biomass in the surface water determines the rate of gross respiration in lakes and thus the relative importance of sediment mineralization in whole lake metabolism. In chapter 1, I present two conceptual models of gross metabolism in lakes to assess the relative importance of the sediment mineralization firstly, as a function of mean depth and secondly, as a function of algal biomass in the surface water.

Fig. 1. Conceptual model of areal hypolinetic oxygen depletion rates (AHOD) and the fate of organic matter in lake hypolimnia of different thickness. The oxidation of organic matter is proportioned between water oxygen consumption and sediment oxygen consumption (SOC) while remaining organic material is accumulated in the sediments (adapted from Charlton 1980).


AHOD
Water Oxygen Demand
Sediment Oxygen Demand
Storage in Sediments
Total Organic Supplies
Total Oxygen Consumption
Hypolimnion Thickness →

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Chapter 1.

Organic matter mineralization rates in lake sediments:
A within and among lake study.

Abstract

Organic matter mineralization rates were measured by the accumulation of DIC + CH_4 in the water overlying intact cores taken from littoral and profundal sediments of 9 Quebec lakes. The variability in areal carbon mineralization is much greater within lakes than among lakes varying in trophy. The rate of organic matter mineralization in littoral sediments is more variable and, on average, 3 fold higher than in the profundal sediments. Sixty per cent of the variation in summer carbon mineralization rates is explained by site depth, a surrogate variable that incorporates the effect of temperature and may also be reflecting substrate quality and/or supply. The lake-specific characteristics most strongly correlated to residuals of the regression with depth are the catchment area to lake area ratio (CA:LA) and the water residence time. In lakes with a larger CA:LA and a shorter residence time the amount and possibly the quality of organic matter settling to the sediments at a given depth may be reduced, resulting in the lower observed organic matter mineralization rates. Mineralization in the sediments is primarily a function of lake morphometry. Total mineralization in the sediments is, not surprisingly, greater in larger lakes but the rate per unit area of lake is smaller, reflecting the decreased importance of the littoral zone. More than half (54-100%) of the DIC + CH_4 produced in the sediments is from the littoral zone. Yet, because of the high oxygen consumption in epilimnetic waters, the littoral sediments account for less than 20% of the gross respiration in epilimnia. The relative importance of the sediments in total respiration in lakes is a function of both the trophy and lake morphometry. A smaller proportion of total respiration occurs in the sediments in eutrophic than in oligotrophic lakes, and in deep lakes the sediments account for a smaller proportion of total respiration than in shallow lakes.

Introduction

The recent interest in the global carbon budget has increased the amount of research on the flux of carbon dioxide (CO_2) and methane (CH_4) from surface waters. Release of these gases provides not only a measure of the flux of carbon but also a measure of the net heterotrophic activity of the community. Carbon dioxide is the end product of both aerobic and anaerobic respiration and, together with CH_4, is also an end product of fermentation. Cole et al. (1994) calculated that 87% of lakes world-wide are a source of CO_2. One interpretation of this efflux of carbon is that heterotrophy exceeds autotrophy in lakes.

In shallow aquatic systems characterized by high sediment area to water volume ratio the sediments may be the primary site for organic matter mineralization. Bacteria are the major decomposers of organic matter in aquatic systems (Fenchel and Blackburn 1979) and they are some two to three orders of magnitude more abundant in the sediment than in the equivalent volume of overlying water (Duarte et al. 1988; Schallenberg et al. 1989; Schallenberg and Kalff 1993). Furthermore, the sediments dominate hypolimnetic metabolism with as much as 85% of oxygen consumption in the hypolimnia of lakes occurring in the sediments (Cornett and Rigler 1987). However, only a few studies have examined the accumulation of dissolved inorganic carbon (DIC) (Rich 1975; Rich and Devol 1978; Rich 1979, 1980) or DIC and CH_4 (Kelly et al. 1988) in the hypolimnia of lakes, and the production (Schallenberg 1992; Ramlal et al. 1993; Sweerts et al. 1986) or flux (Carignan and Lean 1991) of DIC and CH_4 in sediments.

Research on metabolism in lakes has traditionally focused on oxygen consumption (Thienemann 1926; Strøm 1931; Hutchinson 1938; Hargrave 1979; Charlton 1980; Cornett and Rigler 1980, 1987) as aerobic respiration is the most efficient pathway for

organic matter degradation. Originally it was believed that the oxygen demand of hypolimnetic water and sediments could be used as an indicator of the trophic status of lakes. However, neither the rate of areal hypolimnetic oxygen depletion (AHOD) (Cornett and Rigler 1980, 1987) nor the sediment oxygen consumption rate (SOC) is strongly coupled to the algal biomass (chl a) in the mixed layer (Hargrave 1979). The relative stability of the SOC (Graneli 1978) and the increase in AHOD in lakes with thicker hypolimnia, allowed Charlton (1980) to develop a useful conceptual model depicting a decrease in the relative importance of sediments in organic matter mineralization in lakes with thicker hypolimnia. Indeed, Cornett and Rigler (1987) reported lower SOC, calculated as the difference between AHOD and water column respiration, in lakes with thicker hypolimnia.

AHOD is also correlated with hypolimnetic temperature of the hypolimnion (Cornett and Rigler 1987). In stratified temperate lakes the epilimnetic water overlying the littoral sediments is about 10 to 15 ^{o}C warmer than the hypolimnetic water. Temperature is an important factor determining microbial activity in both the water column (White et al. 1991) and the sediment (Graneli 1978; Hargrave 1969). Reported Q_{10} values for sediment oxygen consumption range from 1.3 (Graneli 1978) to 7.6 (Hargrave 1969). Yet, the activity of microbial communities in slurries of profundal sediments is lower in a more shallow lake than a deeper lake, even after correcting for the lower water temperature of the deeper lake (Kelly and Chynoweth 1981).

Substrate quality is argued to be a function of both the source and the refractory nature of the organic material (Wetzel 1983). Exposure of detritus to microbial degradation in the water column and sediment can be expected to deplete detritus of labile components. Autochthonously produced material is considered the preferred substrate for heterotrophs as it is less refractory and is generally higher in nutrient content than

allochthonous terrestrial material. Fine organic matter sedimented in the littoral zone that is not immediately metabolized will be resuspended during high energy periods and ultimately transported to profundal sediments (Davis and Brubaker 1973; Davis 1973; Rowan et al. 1992). As a result profundal sediments are not only characteristically finer than littoral sediments (Rowan et al. 1992) but are also composed of organic matter which has had greater exposure to degradation by bacteria while part of the littoral sediments and subsequently in the water column. Thus, the quality and the autochthonous nature of organic material arriving at the sediment surface could be expected to be higher in the littoral sediments than in profundal sediments. Furthermore, macrophytes and benthic algae also provide substrate for the microbial community of littoral sediments (Wetzel 1990).

The combination of higher temperatures and the higher quality substrate should allow the highest microbial activity to occur in the littoral sediments. Yet, research to date has focused almost exclusively on profundal sediments even though smaller lakes, dominated by the littoral zone, are much more common than deeper pelagic dominated lakes (Wetzel 1990). The influential work of Jones and Simon (1981) contributed to the bias towards pelagic sediments by showing bacteria to be less abundant and less active per gram of dry sediment in littoral than in profundal sediments. However, when expressed per unit area or volume the bacteria are, as expected, more abundant (Duarte et al. 1988; Schallenberg et al. 1989; Schallenberg and Kalff 1993), more active (Ramlal et al. 1993) and more productive (Sander and Kalff 1993) in littoral than profundal sediments.

The DIC + CH_4 release rates from sediment cores taken from the littoral and profundal zones of 9 north temperate lakes were measured to address the following questions: (1) Does lake morphometry affect the rate of carbon mineralization in sediments? (2) What is the relative role of the littoral and profundal sediments in whole

lake sediment mineralization rates? (3) Does the source of the organic material affect the rate of carbon mineralization in the sediments?

Methods

Study area and sampling regime

Nine Quebec lakes in the Eastern Townships (St. Lawrence River Valley) and Laurentians (Canadian Shield) were selected to maximize the range of chl a, water residence time and drainage basin characteristics. The inclusion of the three brown water Laurentian lakes extended the humic range. The study lakes have been used in a number of previous studies (e.g. Duarte et al. 1988; Rowan et al. 1992), providing important background information on their morphometry, sediment characteristics and biology (Table 1).

Each lake was visited between one and four times during the summer and early fall of 1993. Sampling took place during the first two weeks of June, July, August and October. All lakes were stratified during the June sampling. However, polymictic lake Waterloo was completely mixed on the July and August sampling dates with water column temperatures above 20 ^{o}C and lake Brome was mixed to a depth greater than 7 m on the August sampling date. By October all lakes had destratified and cooled to between 7 and 12 ^{o}C.

Three replicate cores were taken from up to three habitats per lake, using 5 cm diameter PVC tube. The habitats were: (1) the profundal sediments of the lake or bay, (2) a littoral area with macrophyte growth, and (3) a littoral area with coarse grained sediments and limited or no macrophyte growth. The profundal sites were sampled with a gravity corer, while cores were collected from the shallow sites by SCUBA. Care was taken to avoid inclusion of large macrophytes or macrofauna and only undisturbed cores were kept for analysis. Cores were capped and returned to the lab on the day of collection.

Table 1. Morphometric, hydrological and biological data for 9 study lakes lakes located in the Laurentians and Eastern Townships of southern Quebec. Morphometric and hydrological data taken from Schallenberg (1992). Chl a is the mean summer concentration (n=number of months) for 1993 (present study).

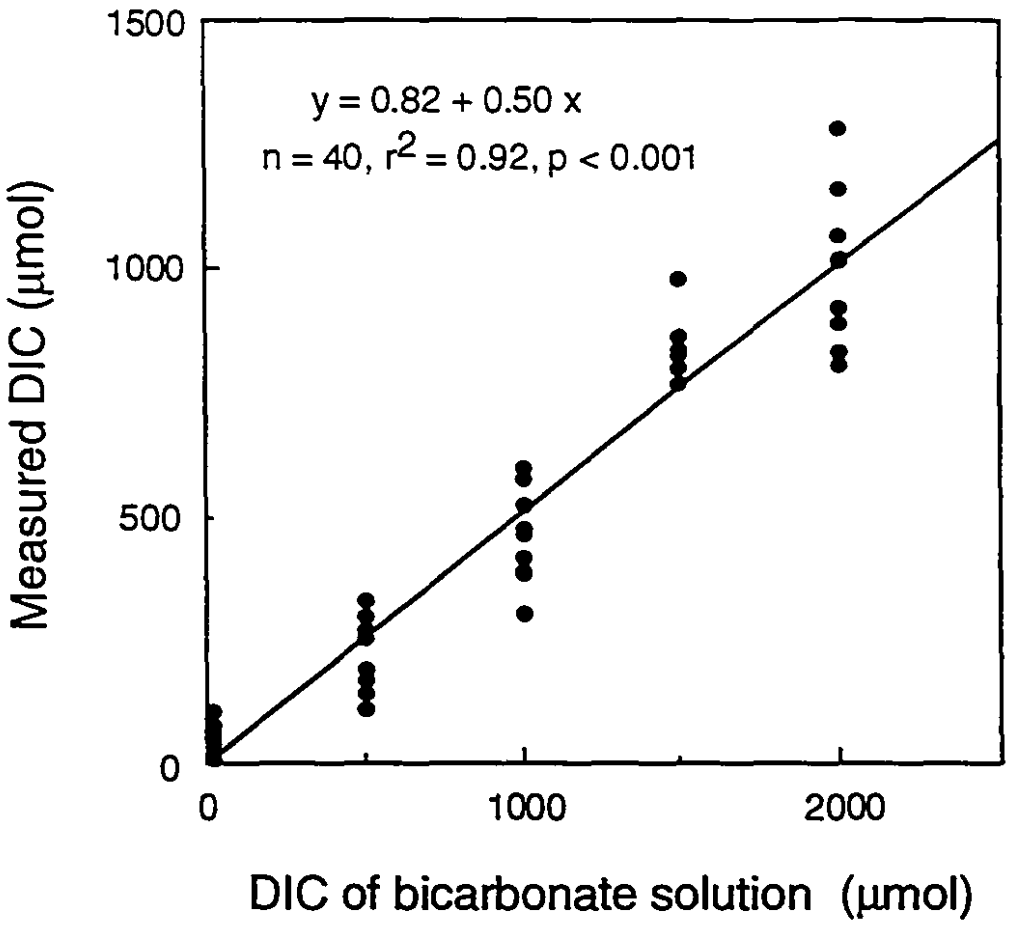
Lake	Mean Depth	Max. Depth	Volume	Drainage Area	Lake Area	Water Residence Time	chl a (n)
	m	m	10^6 m^3	km^2	km^2	yr	µg l^{-1}
Laurentians							
Achigan	12.1	25.0	60.08	90.44	4.98	1.30	1.9 (4)
Croche	4.6	10.0	0.21	0.19	0.19	1.88	2.2 (4)
Cromwell	3.0	9.5	0.25	8.76	0.11	0.06	6.0 (4)
Eastern Townships							
Bowker	23.7	57.2	57.77	7.72	2.44	12.71	0.9 (3)
Brome	5.8	11.5	81.61	185.60	14.17	0.92	8.2 (3)
Hertel	4.7	9.0	1.69	3.30	0.29	0.65	4.6 (2)
Magog	7.7	17.5	70.90	1852.60	9.27	0.08	6.8 (4)
Memphremagog (Green Bay)	.	.	.	.	2.35	.	3.9 (3)
Waterloo	2.9	4.9	4.30	25.00	1.50	0.23	10.9 (3)

Altogether 224 cores were collected and analysed. For each core the carbon mineralization rate of the sediment microbial community, the water content and the organic matter content (g g^{-1} dry weight) of the top centimeter were measured. Organic matter source was assessed by determining the stable carbon isotope ratio ($\delta^{13}C$) and C:N ratio of organic matter in the top centimeter of a subset of the cores.

Carbon mineralization rates

In the laboratory, the cores were sealed with rubber stoppers. A few milliliters of lake water or CO_2 free water was added to the cores so that no air was trapped. Cores were stored in the dark at +/- 2 ^{o}C of the *in situ* temperature. After a one or two day equilibration period, 20 ml samples of the overlying water were removed for analysis of CO_2 and CH_4. The water overlying the sediments was gently mixed before and after sampling, using a magnetic stirring bar suspended from the stopper and the volume of water removed was replaced with CO_2 free water. Every sample was acidified with 2 ml of 0.1N H_2SO_4 to convert bicarbonate to CO_2, and then sparged with 20 ml of He by vigorous shaking for 50 seconds (Stainton et al.1977; Schallenberg 1992). The concentration of CO_2 and CH_4 in 20 ml water samples was determined using a HNU gas chromatograph, with a 0.306 mm x 1.118 m (1/8" x 4') Hayesep D packed column, UHP He carrier gas (30 ml min^{-1}), and a far-UV detector. Gas standards were used for both CO_2 and CH_4. A sparging efficiency for CO_2, of 50%, was determined experimentally using bicarbonate solutions (Fig. 1). This estimate was also confirmed with the method of McAullife (1971). The McAullife method was used to calculate the sparging efficiency of CH_4. Ninety-seven per cent of dissolved CH_4 is extracted by my method, which is the CH_4 extraction efficiency calculated by McAulliffe. The detection limit of this analysis was 0.16 µM for CO_2 and 0.028 µM for CH_4.

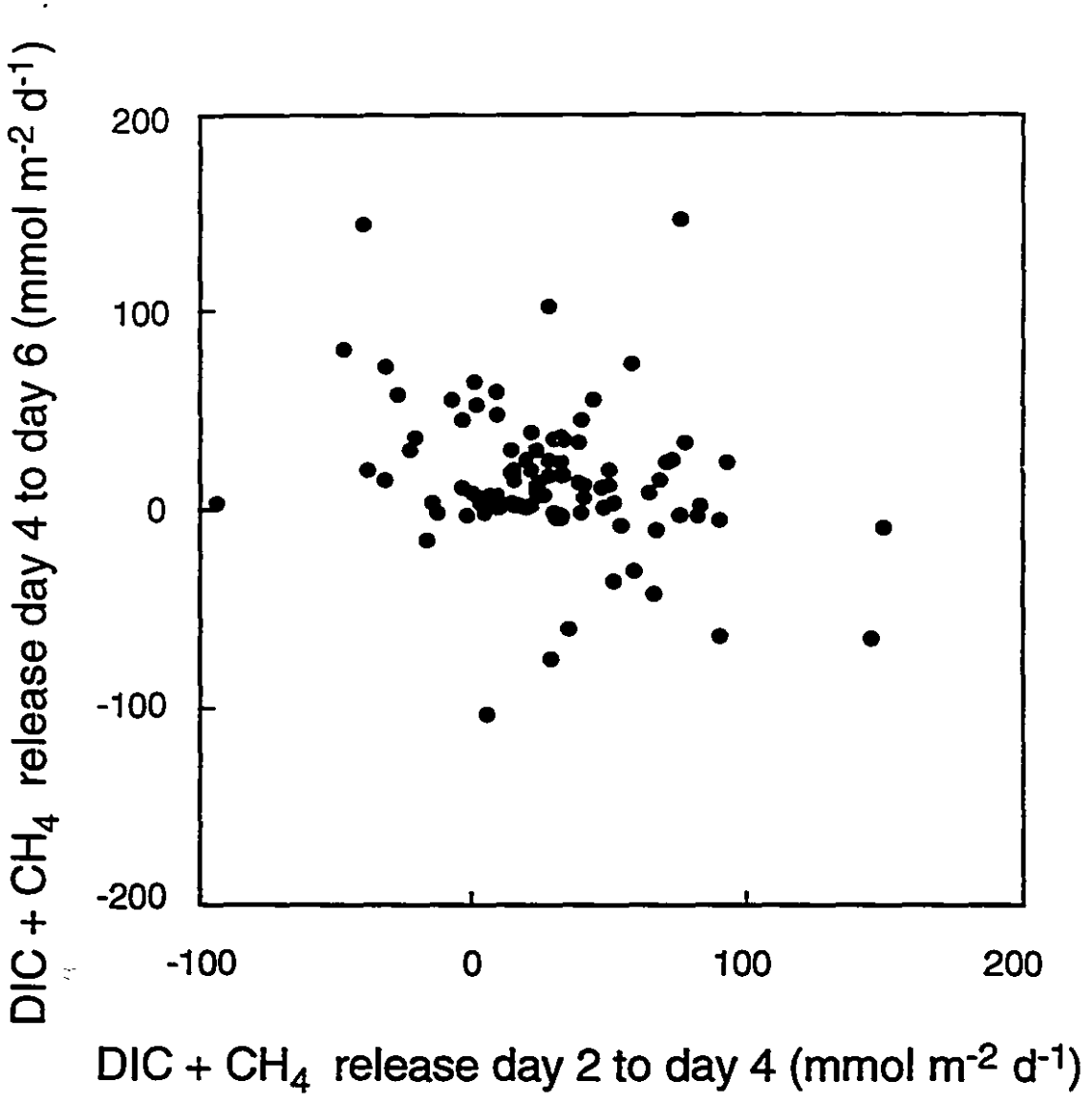
Fig. 1. Standard curve of 20 ml bicarbonate solution acidified with 2 ml of 0.1 N acid and sparged with 20 ml of He. The x axis is the known concentration of carbonate in solution and the y axis is the concentration determined using a gas standard (see methods for protocol). The points represent individual samples run on three separate days. The intercept is not significantly different from zero, and the slope of the regression is the sparging efficiency.


y = 0.82 + 0.50 x
n = 40, r2 = 0.92, p < 0.001
Measured DIC (µmol)
DIC of bicarbonate solution (µmol)
0
500
1000
1500
0
1000
2000

Rates of carbon mineralization were determined from the change in the volume of DIC and CH_4 in the water following 2, 3 or 4 day incubations. For the cores taken in June and July the rates of mineralization were determined over two consecutive 2 day incubations. The consecutive release rates were not well correlated (Fig. 2), and the less variable 4 day incubations were used in analysis for all cores except for 25 cores that were incubated for 3 days. An ANOVA showed there to be no significant effect of 3 and 4 day incubations on the carbon mineralization rates. The detection limits for the DIC and CH_4 accumulation rates are dependent on the volume of water overlying the sediments and the duration of incubation. The method is more sensitive in cores with a smaller volume of water and a longer incubation time. The volume of water overlying the sediment cores ranged from 58 ml to 616 ml. With a 4 day incubation and 58 ml of water overlying the cores, the minimum detectable rates of DIC and CH_4 accumulation were 1.5 and 0.25 mmol m^{-2} d^{-1}, respectively. The detection limits with 616 ml of water overlying the core and only 3 days of incubation was 20.8 mmol m^{-2} d^{-1} for DIC and 3.49 mmol m^{-2} d^{-1} for CH_4. The best estimate of the detection limits, calculated for the mean water volume (327 ml) and a 4 day incubation, are 9.4 and 1.56 mmol m^{-2} d^{-1} for DIC and CH_4, respectively.

Only the net carbon release of DIC + CH_4 was considered since the methods did not protect against the introduction of oxygen during handling and incubation. In the presence of oxygen CH_4 can be oxidized by either chemical reaction or microbial activity. The chemical oxidation of CH_4 to CO_2 will not affect the release of DIC + CH_4 because a mole of CO_2 is produced for every mole of CH_4 oxidized. However, the presence of methanotrophs could result in underestimation of the carbon mineralization rate as methanotrophs fix about 1/3 of the CH_4 consumed with the balance being respired as CO_2 (Håkanson and Jansson 1983). The fixing of carbon by methanotrophs is unlikely to have significantly affected my estimates of organic matter mineralization because CH_4 release

Fig. 2. Release of DIC + CH_4 (mmol m^{-2} d^{-1}) from 120 sediment cores incubated for two consecutive two day incubations at +/- 2 ^{0}C. Approximately 40% of the data are hidden.


200
100
0
-100
-200
-100
0
100
200
DIC + CH4 release day 4 to day 6 (mmol m-2 d-1)
DIC + CH4 release day 2 to day 4 (mmol m-2 d-1)

rates ($\bar{x}$ = 3 mmol m^{-2} d^{-1}) were only about 20% of the release rates of DIC ($\bar{x}$ = 14 mmol m^{-2} d^{-1}). Introduction of oxygen to the incubating cores may also have inhibited organic matter mineralization by strict anaerobes. Accumulation of reduced products in the sediments may have buffered the sediments from the effects of oxygen introduction. These assumptions appear to be warranted as the reported rates of carbon mineralization are comparable to published rates of CO_2 accumulation (Table 7) and oxygen consumption (Fig. 7).

Sediment characteristics and organic matter quality

After determining the mineralization rates, the cores were stored for up to 2 weeks at 4 ^{o}C. The top centimeter was removed from each core using a vertical extruder. Water content of the surface sediment was determined by oven drying at 60 ^{o}C. The dried sediment was ground to homogenize the sample, and subsamples were ashed overnight at 550 ^{o}C to determine the organic content of the sediments. To calculate the areal concentration of organic matter, the bulk density (g ml^{-1}) was calculated from water content and sediment dry weight (Rudd et al. 1986). The densities of water and sediment particulate material were assumed to be 1 g ml^{-1} and 2.6 g ml^{-1}, respectively.

Stable carbon isotope and C:N ratios of organic matter in the top centimeter of sediments were determined for 55 cores using a Europa Scientific Tracermass mass spectrometer interfaced with a Roboprep-CN analyzer. The cores analysed for $\delta^{13}C$ and C:N include both shallow and deep sediment from all 9 lakes. Five to 10 ml of dried sediment was acidified with 10 ml of 2 to 3% phosphoric acid to remove any carbonates from the sediments. The acid sediment mixture was shaken and left overnight to allow the acid to react. The samples were then oven dried at 60 ^{o}C and subsequently ground with mortar and pestle. Enough sediment to contain between 2 and 3 mg of organic matter, was

packed into duplicate titanium capsules. The mean standard error of the $\delta^{13}C$ ratio of the duplicates, expressed as parts per thousand or per ml difference from PDB (Fry and Sherr 1984), was 0.26 ‰ (n=55). And the mean standard error of the C:N molar ratio was 0.40 (n=53). Five cores obtained from a shallow enclosed bay of lake Bowker were removed prior to statistical analysis, as they reflected the particular bay rather than the lake.

Lake and site characteristics

Temperature and oxygen profiles were obtained using an Orion model 840 oxygen meter. Epilimnetic depth was determined as the depth of maximal temperature change. Between 250 ml and 1 L of lake surface water was filtered through A/E Gelman glass fiber filters in triplicate for chl a analyses. Pigment was extracted in 12 ml of ethanol and chl a concentration was determined by the tricolormetric absorption (Bergmann and Peters 1980). Site exposure and area at depth was determined by planimetry using bathymetric maps.

Statistical Analysis

Statistical analysis was performed using SAS. All variables used in correlation and regression analysis were tested for normality. Logarithmic transformation of the morphometric and productivity variables, and arc sin transformation of % organic matter content and % water content were used to normalize the data (Table 2).

Table 2. Summary of the data collected from Eastern Township and Laurentian lakes during June, July and August of 1993. The mean, minimum and maximum values of environmental and biological variables are presented for the profundal and littoral habitats.

	profundal				littoral weed bed				littoral sand				transformation
	n	mean	min	max	n	mean	min	max	n	mean	min	max	
$DIC+CH_4$ (mmol $m^{-2}d^{-1}$)	63	7	-20	24	67	29	-50	75	52	21	-45	112	none
site depth (m)	63	11.5	3.7	35	67	1.8	1.0	5.0	52	1.9	0.6	6	logarithmic
water temperature (°C)	63	11	4	22	67	20	7	26	52	22.0	18	26	none
water content (% dry weight)	48	88	38	99	54	80	49	99	42	44	21	76	arc sin
organic matter (% dry weight)	57	29	2	56	61	20	3	62	50	5	1	27	arc sin
areal organic matter (g ml^{-1})	48	0.29	0.04	0.56	54	0.23	0.4	1.00	42	0.06	0.01	0.19	logarithmic
chl a (µg l^{-1})	21	4.7	0.6	14.5	21	4.7	0.6	14.5	16	4.9	0.6	14.5	logarithmic
exposure (km^2)	23	2.63	0.03	12.77	23	2.39	0.09	7.92	18	3.45	0.29	12.77	logarithmic

Results

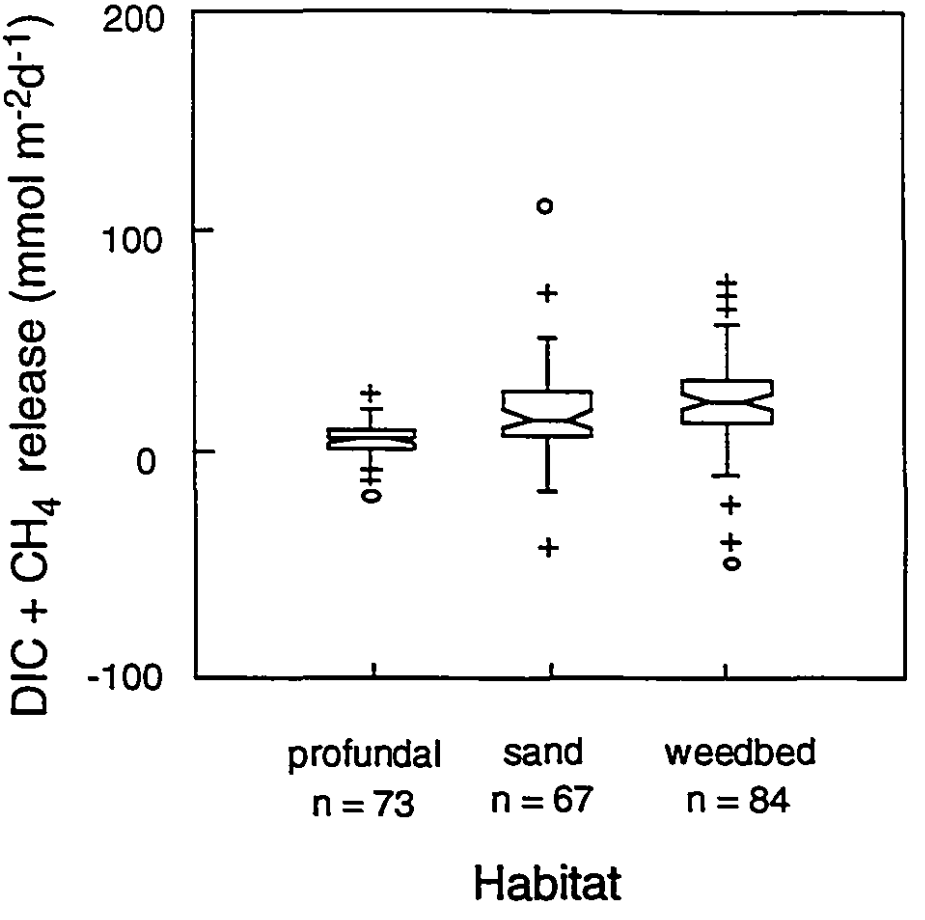
Mean summer phytoplankton biomass (chl a) and lake morphometric attributes varied between 1 and 2 orders of magnitude (Table 1). The variation in sediment carbon mineralization and other sediment attributes are given in Table 2. The water content of the sediments varied between 21 and 99 % and the organic content from 1 to 62 %. Cores from the littoral sand habitat had the lowest mean value and greatest range in water and organic matter content, while cores from the profundal habitat had the highest mean values and smallest range in water and organic matter content. The range in the stable carbon isotope signatures of organic matter in the top centimeter was greater for cores collected in the littoral habitats than in the profundal habitat. Finally, the carbon mineralization rates in the individual cores ranged from -50 to 112 mmol $m^{-2}d^{-1}$ and were higher and more variable in the sand and weedbed habitats than in the profundal habitat.

The ANOVA shows that the main source of variability in carbon mineralization rates was among habitats rather than among lakes (Table 3). Carbon mineralization rates differ significantly among the three habitats, with larger and more variable carbon mineralization rates in the sand and weedbed habitats than in the profundal habitat (Fig. 3). The ANOVA further showed there to be a weak effect of time of year. Organic matter mineralization rates in the summer months (June, July and August) were not significantly different from each other but were higher than in October. The mean summer carbon release rate (17.0 +/- 0.1 mmol m^{-2} d^{-1}) is almost twice the mean release rate in October (8.6 +/ 0.4 mmol m^{-2} d^{-1}). While the effect of lake in the ANOVA was not significant on its own the interaction between month and lake was significant, suggesting that seasonal effects were not the same in all lakes. Only the cores taken in June, July and August are considered in the present analysis, due to the high inter-season variability in carbon release rates.

Table 3. An analysis of variance of the importance of sampling date and habitat on carbon mineralization rates in individual cores. The cores were collected during the summer and fall of 1993 from 9 lakes in the Eastern Townships and Laurentians of southern Quebec. The three habitats are: profundal, littoral weedbed and littoral sandy. A Tukey test indicates a significant difference among all three habitats.

Source	DF	Type III SS	MS	F Value	P
Model	53	37149.59	700.94	2.71	0.0001
Lake	9	1340.63	148.96	0.58	0.81
Habitat	2	3251.11	1625.55	6.29	0.0023
Month	3	2047.38	682.46	2.64	0.051
Lake*Habitat	13	3584.70	275.75	1.07	0.29
Habitat*Month	6	1932.47	322.08	1.25	0.29
Lake*Month	20	11813.44	590.67	2.28	0.0023
Error	170	43960.14	258.59		
Total	223	81109.72			

Fig. 3. Box plot of carbon dioxide plus methane release from individual cores collected in June, July and August. The horizontal bars indicate the median, 25th and 75th percentiles, the + and o symbols indicate outside values and the notches represent the 95% confidence interval of the median. A Tukey multiple range test finds the mean carbon mineralization rate among all three habitats to be significantly different.


200
100
0
-100
DIC + CH_4 release (mmol $m^{-2}d^{-1}$)
profundal
n = 73
sand
n = 67
weedbed
n = 84
Habitat

Temperature was positively correlated with carbon mineralization rates (Table 4, Fig. 4). Mineralization rates were furthermore negatively correlated with site depth, but this is not easily interpreted as depth and temperature co-vary (Table 5). Temperature was probably the principal determinant of carbon mineralization rates. However, depth explained more of the variability in carbon mineralization rates (Table 4), and is, consequently, more than a simple surrogate for temperature.

Physical characteristics of the sediment, such as water content and organic matter content, were not strongly coupled to the rate of mineralization despite the wide range of water and organic matter content observed. Nor were the measures of physical structure correlated with the residuals of the temperature and depth regressions of carbon mineralization, possibly because of the autocorrelation of depth, temperature and physical structure. Although the sampling regime was designed to include shallow sediment cores from both fine grained organic weedbed habitats and coarse grained inorganic sand habitats, there remained weak correlations between site depth and water and organic matter content (Table 5).

The residuals of the regression between mean summer carbon mineralization rates and site depth were negatively correlated with the catchment area to lake area ratio (CA:LA), and positively correlated with the flushing rate. These two variables are themselves highly correlated and may be acting as surrugates for the amount of organic material supplied to the sediments, as flushing rate is negatively correlated with organic matter retention (Groeger and Kimmel 1984). The variance in log transformed carbon mineralization rates explained by the model increases from 60 to 76% (model 10, Table 4) when CA:LA was included in a multiple regression with site depth. I tested the predictive power of this model with data collected from the literature (Fig. 5).The standard error of

Table 4. Stepwise regression models of DIC plus methane release rates (mmol m^{-2} d^{-1}) from sediment cores, incubated in the dark, as a function of environmental factors, based on data collected from 9 Quebec lakes. Models 1 and 2 represent the individual cores; models 3 and 4 are based on mean monthly release rates per habitat; models 5, 6 and 7 are based on mean summer release rates per habitat, and models 8, 9 and 10 are based on the logarithim of mean summer release rates per habitat. Temp=incubation temperature (°C), depth=log site depth (m), CA:LA=ratio of catchment area to lake area.

y	n	intercept x-coefficient	std error	r^2	p
Individual cores					
Model 1	224				
constant		0.52	3.01		ns
Temp		1.05	0.18	0.14	0.0001
Model 2	224				
constant		24.02	1.81		0.0001
depth		-15.02	2.91	0.11	0.0001
Habitat mean by month					
Model 3	78				
constant		0.83	3.34		ns
Temp		1.03	0.20	0.26	0.0001
Model 4	78				
constant		23.56	2.18		0.0001
depth		-13.75	3.36	0.18	0.0001
Summer mean					
Model 5	25				
constant		0.33	5.19		ns
Temp		1.05	0.29	0.36	0.001
Model 6	25				
constant		27.92	2.47		0.0001
depth		-18.40	3.57	0.54	0.0001
Model 7	24				
constant		29.55	2.44		0.0001
depth		-19.53	3.20	0.52	0.0001
CA:LA		-0.069	0.022	0.67	0.01
Log summer mean					
Model 8	25				
constant		0.54	0.13		0.001
Temp		0.036	0.007	0.51	0.0001
Model 9	25				
constant		1.47	0.07		0.0001
depth		-0.58	0.09	0.63	0.0001
Model 10					
constant	24	1.57	0.06		0.0001
depth		-0.62	0.08	0.60	0.0001
CA:LA		-0.002	0.0006	0.76	0.005

Fig. 4. Water temperature *versus* monthly mean carbon mineralization rate in the profundal, littoral weedbed and littoral sandy sites. The intercept is not significantly different from zero. The change in the carbon mineralization rate between 10 and 20 ^{o}C is approximately 2 fold (Q_{10}=1.9). Nine data points are hidden from view.

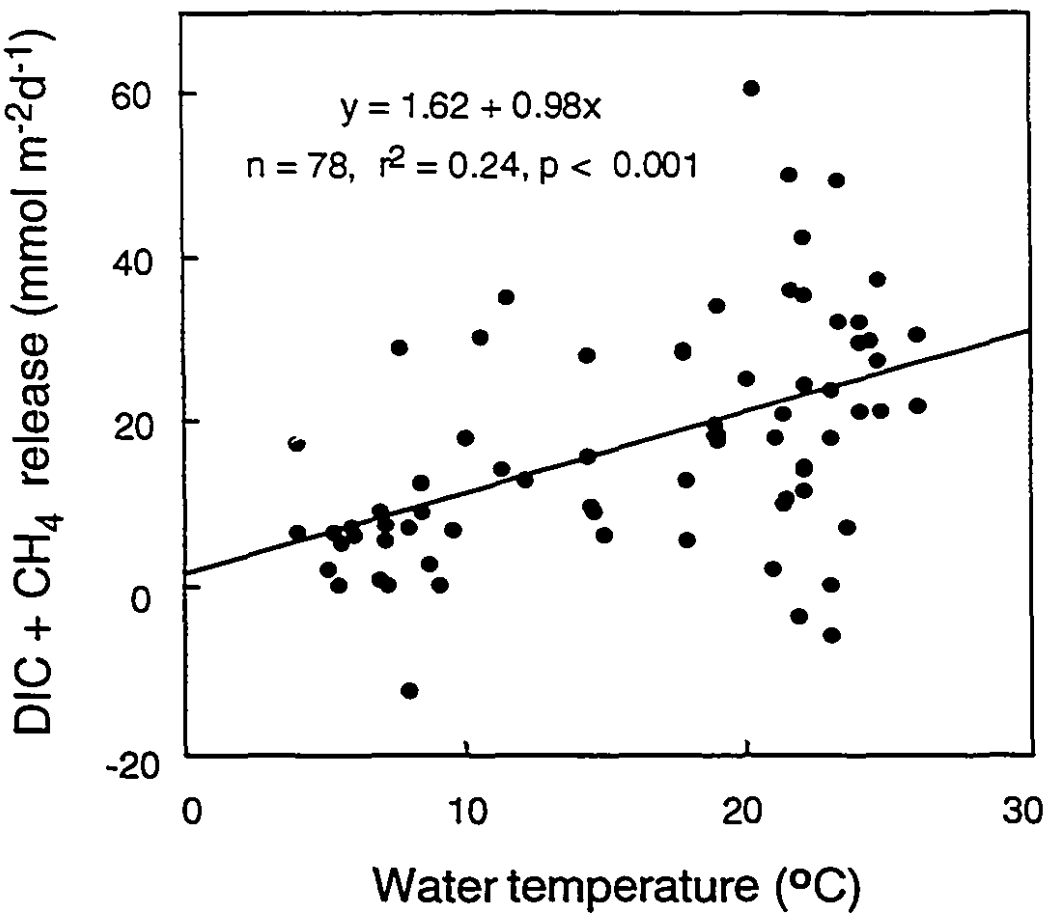
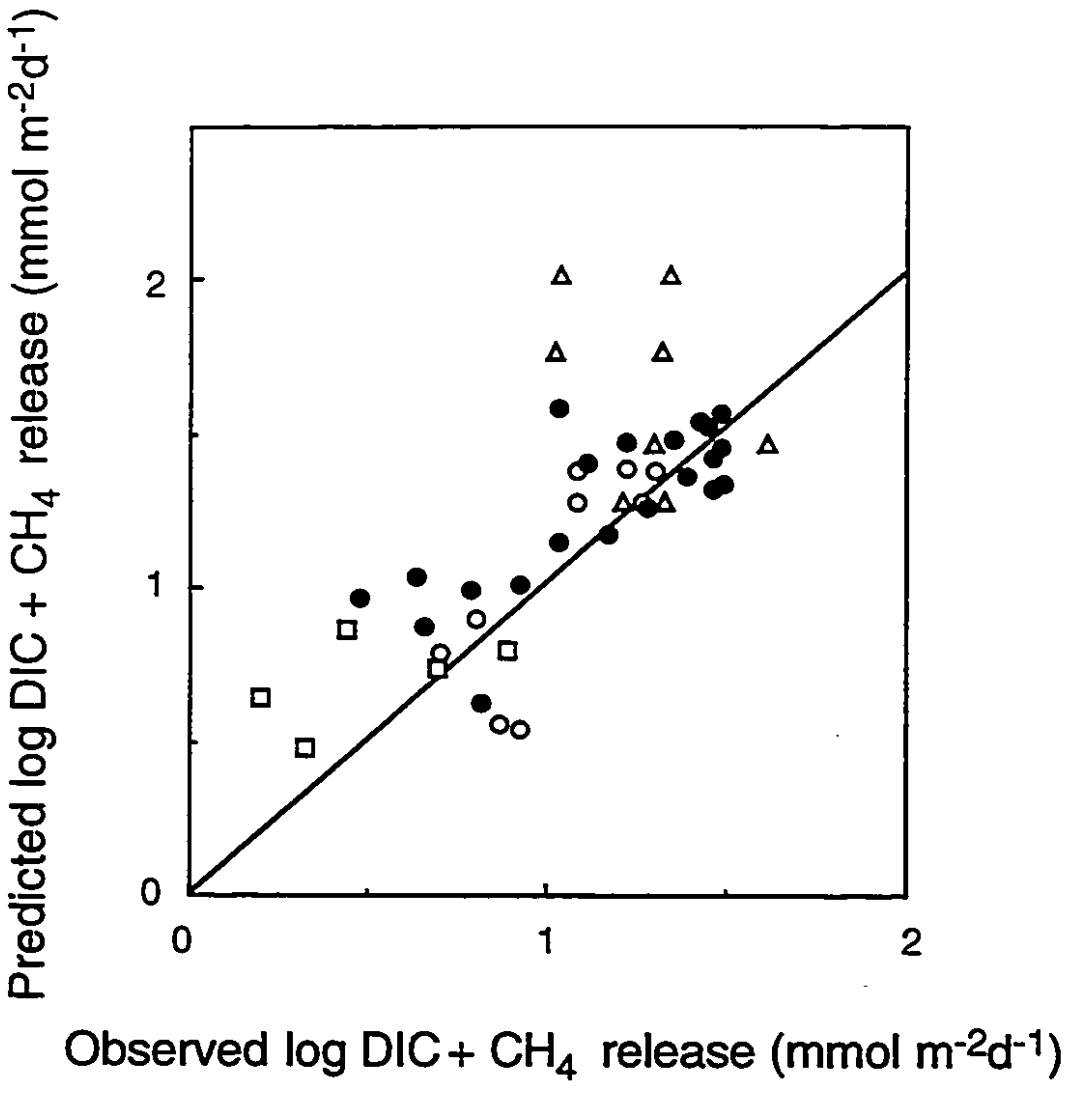

y = 1.62 + 0.98x
n = 78, r2 = 0.24, p < 0.001
DIC + CH4 release (mmol m-2d-1)
60
40
20
0
-20
0
10
20
30
Water temperature (°C)

Table 5. Pearson correlation matrix showing the significant correlations between the monthly average rates of DIC plus methane release from sediment cores and environmental variables in the nine study lakes. The number of samples (n) is presented immediately below the correlation coefficients (r).

* $p<0.05$, ** $p<0.001$, *** $p<0.0001$.

	incubation temperature (°C)	site depth (m)	chl a ($\mu g\ l^{-1}$)	water content (% dry weight)	lake area (km^2)	catchment area/ lake area
$DIC+CH_4$ ($mmol\ m^{-2}\ d^{-1}$)	0.51*** 78	-0.42*** 78	.	-0.29* 66	.	.
incubation temperature (°C)		-0.62*** 79	.	-0.51*** 67	0.43*** 78	.
site depth (m)			-0.26* 72	0.49*** 67	-0.23* 78	.
chl a ($\mu g\ l^{-1}$)				.	.	0.33* 72
water content (% dry weight)					-0.54*** 66	.
lake area (km^2)						0.27* 79

Fig. 5. Observed *versus* predicted (model 10, Table 4) carbon mineralization rates. Log carbon mineralization is predicted from the water depth above the sediment and the catchment area to lake area ratio ($n=24$, $r^2=0.76$, $p<0.001$). My data (●) are the mean carbon release rates from cores collected in June, July and August. The test data are release rates estimated from undisturbed cores incubated in the dark (□ Schallenberg 1992; ○ Ramlal et al. 1993) and *in situ* opaque benthic chambers (Δ Sweerts et al. 1986). The four obvious outliers are sites that are less than a meter deep.


Predicted log DIC + CH_4 release (mmol $m^{-2}d^{-1}$)
Observed log DIC + CH_4 release (mmol $m^{-2}d^{-1}$)
0
1
2
0
1
2

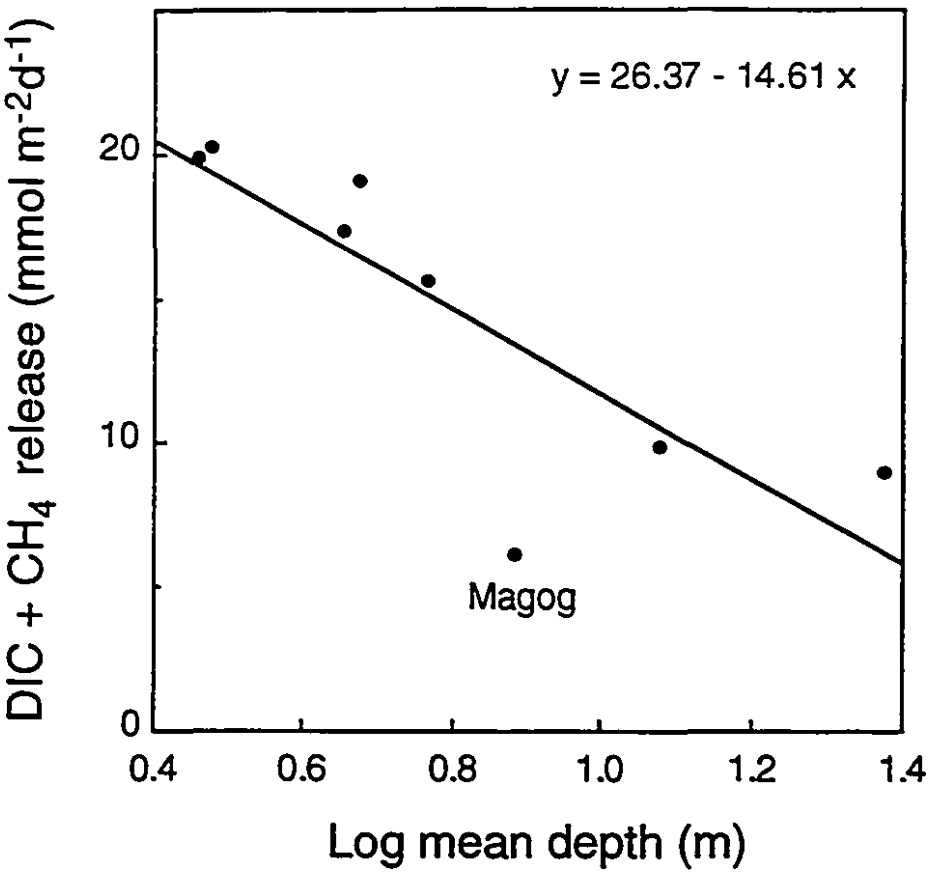
the estimate for the data used to generate the model is 0.04 (n=21), and the standard error of the estimates for the test is 0.11 (n=22). The literature data were measured using dark incubation of undisturbed cores (Schallenberg 1992; Ramlal et al. 1993) and opaque *in situ* benthic chambers (Sweerts et al. 1986). Four sites in the Sweerts et al. (1986) study were collected from sediments overlain by less than a meter of water (20 and 50 cm), beyond the range of the model, and were overestimated by the model. The standard error of the estimate for just those test at a depth greater than 1 m, is 0.05 (n=18). The strength of the predictive model attests to the accuracy of the present estimates despite the recognized uncertainty in the calibration of the methods (Fig. 1 & 2).

Lastly, whole lake carbon mineralization rates were calculated by integrating model 10 (Table 4) over area at depth. The total organic matter mineralization in the sediments during the summer ranged over 2 orders of magnitude among the 8 study lakes for which the bathymethetric and morphometric data were complete (Table 6). The mean areal mineralization rates in the sediments of a lake with a mean depth of 5 m is twice that of a lake with a mean depth of 15 m (Fig. 6). Deeper lakes, with a greater sediment area naturally exhibited a higher whole lake sediment flux but at the same time a lower flux per unit area than in shallow lakes, reflecting the greater proportion of the sediments overlain by epilimnetic water in the latter. Carbon mineralization in littoral sediments, defined as those overlain by epilimnetic water, accounted for between 54 and 100% of the mineralization in lake sediments.

Table 6. Total summer sediment organic matter mineralization in the sediments of 8 southern Quebec lakes, calculated by integrating model 10 over lake area at depth, obtained from bathymetric maps. A comparison of the mineralization in the sediments overlain by epilimnetic water to the total sediment mineralization of the whole lake demonstrates the disproportionate importance of the shallow sediments in carbon mineralization.

Lake	mean depth	catchment area: lake area	Total summer mineralization	mean depth of epilimnion	epilimnetic area / lake area	epilimnetic mineralization
	m		10^6 mol	m	%	%
Achigan	12.1	18.16	4.4	8	34	58
Bowker	23.7	3.16	0.9	6	25	54
Brome	5.8	13.10	19.6	7	73	85
Croche	4.6	3.80	0.3	3	46	69
Cromwell	3.0	79.64	0.2	2	60	82
Hertel	4.7	11.38	0.5	6	98	99
Magog	7.7	199.85	5.3	9	68	84
Waterloo	2.9	16.67	2.7	5	100	100

Fig. 6. Mean areal flux of carbon from lake sediments *versus* the mean depth of the lakes. The carbon mineralization rate is calculated from the depth weighted total summer flux (Table 6).


y = 26.37 - 14.61 x
DIC + CH_4 release (mmol $m^{-2}d^{-1}$)
20
10
0
0.4
0.6
0.8
1.0
1.2
1.4
Magog
Log mean depth (m)

Discussion

Sediment carbon mineralization rates vary over time and space. The spatial variation in mineralization rates is large and is larger among habitats within lakes than among the lakes varying considerably in trophy (Table 3). The discussion therefore focuses initially on the processes that determine the areal organic matter mineralization within lakes followed by a consideration of the principal determinants of the among lake variability, and the relative importance of sediment mineralization in whole lake metabolism.

The range in DIC + CH_4 release among the individual cores in the present study is greater than the range of DIC release from freshwater sediments reported in the literature (Table 7). Despite difference in physical energy, sources of carbon, and availability of oxidants, the carbon mineralization rates in shallow marine sediments are surprisingly similar to their freshwater counterparts. Since the measures of DIC and CH_4 release are combined in the present study, it is not surprising that the estimates of organic matter mineralization exceed the reported fluxes of DIC from lake sediments. Although CH_4 accumulation was on average only 20% of the total flux in my cores, the limited literature indicates that CH_4 may account for as much as 42% of DIC + CH_4 regeneration in lake hypolimnia (Kelly et al. 1988). Methanogens are less active in marine sediments because of competition from sulphate reducers (Capone and Kiene 1988) and the present estimates of carbon mineralization are consequently more directly comparable to DIC release from marine sediments.

The lowest carbon mineralization rates in individual cores were lower than those previously reported (Table 7), with carbon consumed in 10% of the cores of the present study. Consumption of DIC in lake sediments and hypolimnia has been noted before but

Table 7. Summary of literature data on DIC and methane release from sediment cores and benthic chambers incubated in the dark.

Source	Site	DIC	DIC + CH_4
		mmol m^{-2} d^{-1}	
Marine			
Therkildsen and Lomstein 1993	Norsminde Fjord, Denmark	17 - 132	-
Anderson et al. 1986	Gullmarsfjorden, Western Sweden	19.1 +/- 1.1	-
Blackburn et al. 1988	marine ponds, Eilat, Isreal	75 - 104.2	-
Kristensen et al 1992	Indus Delta, Pakistan	-104 - 50	-
Freshwater			
Pulliam 1993	wetlands, Georgia	1.66 - 20.6	-
Hedin 1990	HBEF stream, New Hampshire	2.2 - 28.4	-
Sweerts et al. 1986	Lake 302S, Manitoba	11 - 43	-
Ramlal et al. 1993	3 Manitoba lakes		
	2 - 5 m	3 - 25	-
	12 - 46 m	3 - 11	-
Ramlal et al. 1994	Lake 18, North West Territories	32.4 - 46.7	-
Schallenberg 1992	Eastern Townships, Quebec		
	6 - 35 m	-	1.6 - 7.7*
present study	Eastern Townships and		
	Laurentians, Quebec		
individual cores	littoral 1-5 m	-	-50 - 112
	profundal 6-35 m	-	-20 - 24
mean monthly release by site	littoral 1-5 m	-	17- 60
	profundal 6-35 m	-	-3.0 - 14

*corrected for CO_2 sparging efficiency (Fig. 1)

may well be underreported, with such carbon consumption attributed to experimental error in the absence of a better explanation. Reported DIC consumption in individual shallow marine cores incubated *in situ* has been attributed to algal carbon fixation (Dollar et al. 1991). In the present study the carbon consumption cannot be the result of photosynthesis since the cores were incubated in the dark. Low ratios of DIC release to O_2 consumption (RQ) have been reported in both shallow marine sediments (Hansen and Blackburn 1991) and the hypolimnion of Lawrence Lake (Rich and Devol 1978). Both anaerobic autotrophic production and the precipitation of carbonates were suggested, but not demonstrated, as reasons for the low RQ values. Although there was no evidence of carbonate precipitation in any of the present cores, it is plausible, given the strong redox gradients in sediments, that there is sufficient chemoautotrophic carbon fixation at the sediment oxycline to result in carbon consumption on small spatial and temporal scales. Yet, there was net carbon consumption in only 3 sites when the DIC + CH_4 release rates for replicate cores were averaged, and a net efflux of carbon was observed from all the sites when averaged over June, July and August.

The DIC + CH_4 release rates were both larger and more variable in the weedbed and sand habitats than in the profundal sediments (Fig. 3). This is reflected in a three times higher standard deviation of the carbon mineralization rates of replicate cores in littoral sites than in the profundal sites. Littoral habitats were also more variable, both in physical characteristics of the sediment and temperature (Table 2). Higher variability in physical characteristics and a resulting need for a greater number of replicate cores in shallow sediments has been noted previously (Håkanson and Jansson 1983; Rowan et al. 1995).

The water overlying the littoral sediments during the summer months was between 10 and 15 ^{o}C warmer than the hypolimnetic water. Such large differences in temperature can be expected to have dramatic effects on the microbial activity in that most biological

reactions have a Q_{10} between 2 and 3. Strong temperature effects have been noted for both AHOD (Cornett and Rigler 1987) and bacterial production in marine and freshwater planktonic communities, particularly at temperatures lower than 20 ^{o}C (White et al. 1991). Reported Q_{10} values for sediment oxygen consumption range from 1.3 (Graneli 1978) to 7.6 (Hargrave 1969), with higher values over lower temperature ranges. The estimated Q_{10} between 10 and 20 ^{o}C for carbon mineralization in the present sediments is 1.9 (Fig. 4). There is greater variability in mineralization at higher temperatures suggesting that at these temperatures factors other than temperature are limiting the rate of organic matter decomposition by the benthic microbial community.

During the summer months site depth is a better predictor of carbon mineralization rate than the temperature of the overlying water (Table 4). The relationship between mean summer carbon mineralization rate and site depth corresponds surprisingly well to the equivalent models for sediment O_2 consumption (SOC) compiled by Campbell (1984) (Fig. 7). Oxygen consumption by both marine and freshwater sediments is inversely related to depth. The slopes of the regressions predicting SOC from site depth are not significantly different between systems even though the rates of O_2 consumption are an order of magnitude higher in marine sediments. Likewise, the slope of the regression predicting carbon mineralization rate from site depth in the present study is also not significantly different from the slopes of the regressions predicting SOC. The thickness of the overlying water column has the same effect on the SOC of marine and lake sediment and, at least in lakes, has the same effect on both the aerobic and anaerobic communities as the DIC + CH_4 release rates are a constant proportion of the SOC rates.

A comparison of the intercept of the regression line predicting mean summer carbon mineralization from the site depth (model 9, Table 4) with the intercept of the respiratory quotient (RQ; mmol DIC + CH_4 produced: mmol O_2 consumed) of 0.68

Fig. 7. Sediment carbon release and oxygen consumption rates *versus* site depth. The carbon mineralization rates are the mean summer release rates for the Quebec lakes (model 9). Sediment oxygen consumption rates were obtained from 17 freshwater and 10 marine studies compiled by Campbell (1984). The slopes of the regressions are not significantly different. The ratio of the intercepts, mmol C released: mmol O_2 consumed in lake sediment, yields an RQ of 0.68.

○ Lake sediment O_2 consumption,

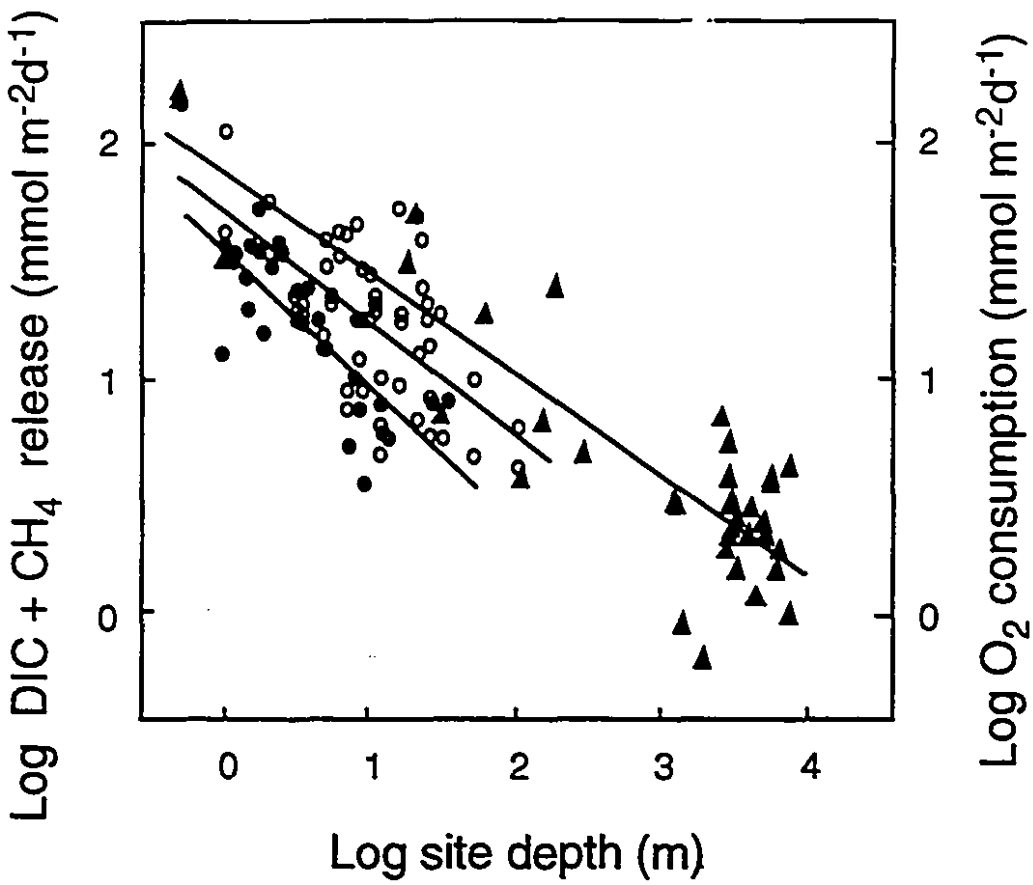
log (SOC) = 1.64 - 0.48 * log (site depth), n=59, r^2=0.42, p<0.001

▲ Marine sediment O_2 consumption,

log (SOC) = 1.80 - 0.43 * log (site depth), n=37, r^2=0.77, p<0.001

● Lake sediment carbon mineralization (present study),

log (DIC + CH_4) = 1.47 - 0.58 * log (site depth), n=25, r^2=0.62, p<0.001


Log DIC + CH_4 release (mmol $m^{-2}d^{-1}$)
Log O_2 consumption (mmol $m^{-2}d^{-1}$)
Log site depth (m)
0
1
2
3
4

(Fig. 5). Reported RQ (mmol of CO_2 produced: mmol O_2 consumed) values for the plankton are typically less than 1, with 0.85 being the most quoted value under aerobic conditions (Wetzel 1983). The present RQ value, although not significantly different from 1, suggests that the sediment microbial community is using low quality substrate because the mineralization of high quality organic matter requires less O_2 than the mineralization of low quality material. However, RQ values computed for mixed aerobic and anaerobic communities cannot be simply interpreted as an indicator of substrate quality. Rich and Devol (1978) reported a range in RQ values from 0.4 to 10.8 for the hypolimnia of 5 North American lakes. In all but one of the lakes the quotients were greater than 1, suggesting that hypolimnetic microbial communities are typically dominated by anaerobes. In Lawrence lake O_2 consumption exceeded DIC production. There the lowest RQ value was observed in the early summer, and the authors proposed that chemical O_2 consumption by reduced products accumulated during the previous stratified season was responsible for elevated rates of O_2 consumption. This explanation is plausible as more recent work has shown that as much as 50% of total O_2 consumption in freshwater sediments can result from chemical demand (Adams et al. 1982; Drabkova 1983; Adams and van Eck 1988; Sweerts et al. 1991). Introduction of oxygen to the incubating cores may also have resulted in temporary inhibition of anaerobic populations such as Dsulv (Cole pers. com.). Even so, the present RQ values should, if anything, overestimate the quality of the substrate available as the estimates of carbon mineralization include not only CO_2 but also CH_4 release. Furthermore, a comparison of seasonal means minimizes the potential for an underestimation of substrate quality resulting from chemical O_2 demand. It is, therefore, reasonable to conclude that the sediment microbial community in these Quebec lakes is confronted by substrate of generally low quality.

The observed negative correlation between depth and SOC in both marine and freshwater systems has been interpreted as the result of a decrease in both the quality and

the quantity of organic matter reaching deeper sediments (Hargrave 1969; Jørgensen 1983). Exposure of organic matter to microbial decompositon in the water column not only reduces the amount of organic matter that reaches the sediments, but also depletes the sedimenting organic material of labile components. In shallow areas of lakes deposition of particulate material occurs throughout the summer, but fine particulate matter is resuspended during high energy periods (Davis and Brubaker 1973; Davis 1973; Rowan et al.1992) and ultimately accumulates in profundal areas (Rowan et al. 1992). The resuspended material has had greater exposure to degradation first by the microbial communities of the warm littoral sediments and second by the water column, and should be more refractory upon its final deposition in the profundal sediments. Indeed, a lower microbial activity has been observed in slurries of profundal sediment in the more shallow Frain's Lake than the deeper Third Sister Lake (Kelly and Chynoweth 1981). Furthermore, macrophytes and benthic algae provide fresh substrate for the microbial community of littoral sediments (Wetzel 1990).

Autochthonously produced organic matter is considered to be the more labile fraction of the organic material in lakes (Wetzel 1983). However, neither of the measures of organic matter source (C:N and $\delta^{13}C$ ratios) were strongly correlated with the rate of DIC + CH_4 release. The sediment microbial community is most active in the difficult to sample upper few millimeters (Novitsky 1983), and C:N and $\delta^{13}C$ ratios of the organic matter in the top centimeter may well be too coarse a measure to assess the substrate available to bacteria at the sediment surface. However, even if the two measures of organic matter quality were inappropriate the algal biomass in the water column above would be expected to affect sediment mineralization rates if indeed the autochthonously produced organic matter is an important source of substrate for the sediment microbial community. No correlation between algal biomass, expressed by volume or per unit area, and the sediment areal carbon mineralization rates or the residuals of the regression predicting

carbon mineralization rates from site depth was observed. It appears that factors other than trophy strongly influence sediment carbon mineralization rates.

The lake-specific characteristics most strongly correlated to the residuals of the regression with depth are the catchment area to lake area ratio (CA:LA) and the water residence time (Table 4). These two variables are interchangeable and appear to be acting as surrogates for the amount of organic matter being supplied to the sediments. While larger catchments provide the receiving lakes with more organic matter, the export per unit area of catchment is lower than for smaller catchments (Rasmussen et al. 1989), and the more rapid flushing of these same lakes decreases the retention of organic matter (Groeger and Kimmel 1984) and potentialy the organic matter supply to the sediments. There may also be a greater resuspension of sediment organic material in the more quickly flushing lakes. Both these mechanisms could contribute to a reduced supply of organic material to the sediments in rapidly flushed lakes, and possibly explain the reduced sediment mineralization rates.

Given the importance of site depth and CA:LA ratio in determining the areal carbon mineralization rates in the sediments, lake and catchment morphometry are necessarily important determinants of the total and the mean areal mineralization rate in the sediments at the whole lake scale. The higher average areal rate observed in shallow lakes reflects (Fig. 6) the proportionally greater area of the littoral sediments (Wetzel 1990). The computed mean areal rate of organic matter mineralization in the sediments of a lake with a mean depth of 5 m is almost twice that of a lake with a mean depth of 15 m (Fig. 6). At the whole lake scale the carbon mineralization in the littoral sediments, overlain by warmer epilimnetic water, accounts for over half of the mineralization in the sediments, even in the deepest lake, Bowker, where the epilimnetic water covers only 25% of the lake bottom (Table 6). Ramlal et al. (1993) too observed elevated rates of DIC + CH_4 release from

shallow cores and argued for the importance of shallow sediments in organic matter mineralization. The present analysis confirms the much neglected littoral sediments as the most important zone of organic matter mineralization in lake sediments.

The last issue to be addressed is the importance of sediment mineralization at the whole lake scale relative to metabolism in the water column. Cornett and Rigler (1987), also working on southern Quebec lakes, reported that between 34 and 84% of the O_2 consumed in the hypolimnia was by the sediments. They found that the proportion of the oxygen consumption in the hypolimnetic water column was a function of the hypolimnetic thickness, in agreement with the conceptual model presented by Charlton (1980). The model of Charlton depicts decreasing rates of organic matter mineralization and a decreasing importance of the mineralization in the sediments relative to the water column with increased hypolimnetic thickness. The present analysis supports this interpretation and extends it beyond hypolimnia to whole lakes. Not only is the sediment area to water volume ratio higher in shallow lakes, allowing for a greater proportion of lake metabolism in the sediments but the mean areal rate of organic matter mineralization too is higher in shallow than in deep lakes. However, the relative importance of the littoral sediments to respiration in epilimnia is considerably less than the profundal sediments in the hypolimna. Respiration in lakes is dominated by the epilimnetic water during summer stratification because of the large planktonic biomass. Del Giorgio and Peters (1993) measured gross rates of O_2 consumption in the epilimnetic waters to be between 6 and 29 mmol m^{-3} d^{-1}. These rates are much greater than the oxygen consumption rates of 0.5 to 6 mmol m^{-3} d^{-1} reported in the hypolimnetic waters by Cornett and Rigler (1987). Sediment mineralization (assuming a RQ=1) accounted for a modest 2 to 18% of the total respiration in the epilimnia of the 4 lakes included in both the present study and the study by del Giorgio and Peters (1994).

Despite the acknowledged importance of lake morphometry in determining the mineralization of organic matter in lake sediments, the relative importance of the sediments in lake respiration is a function of both morphometry and trophy. Based on models of epilimnetic and hypolimnetic oxygen consumption, and my own model of sediment mineralization, all of which were developed for the lakes of southern Quebec, the proportion of gross respiration occurring in the sediments can be modelled as a function of both morphometry and trophy (Fig. 8). The gross respiration of epilimnetic waters is positively correlated with chl a in the surface water (del Giorgio and Peters 1994), and as a result the proportion of whole lake metabolism occurring in the sediments is greater in oligotrophic lakes than eutrophic ones (Fig. 8D). Assuming a mean depth of 10 m, mineralization in the sediments will account for roughly 8% of the total mineralization in eutrophic lakes (chl a = 30 $\mu g\ l^{-1}$) and as much as 33% in oligotrophic lakes (chl a = 0.3 $\mu g\ l^{-1}$). At the same time, for a given algal biomass, the proportion of whole lake respiration occurring in the sediments will vary as a function of mean depth of the lake. In a mesotrophic lake (chl a = 3 $\mu g\ l^{-1}$) with a mean depth of 30m roughly 5% of the total respiration will occur in the sediments, while with a mean depth of 3m, 26% of the total respiration will occur in the sediments (Fig. 8C).

In summary, the modest, but far from negligible, role of the sediments in whole lake metabolism attests to the dominant role of epilimnetic water in primary production and community respiration. Although the relative importance of the sediments in total respiration is a function of lake trophy, sediment organic matter mineralization is independent of primary production in the surface water. Instead, the rate of mineralization in the sediments is primarily a function of the depth of the water column, with whole lake sediment mineralization dominated by the little studied littoral sediments. As shallow lakes, with large littoral zones, dominate the landscape (Wetzel 1990), littoral sediment can be expected to dominate the sediment organic matter mineralization of the majority of lakes.

Fig. 8. Empirically based conceptual model of respiration in lakes. Total respiration is the sum of epilimnetic mineralization (mmol O_2 m^{-2} d^{-1}), calculated from data presented in del Giorgio and Peters (1993), hypolimnetic water column respiration (mmol O_2 m^{-2} d^{-1}), calculated as a percentage of the areal hypolimnetic demand (AHOD) from Cornett and Rigler (1987), and the mean areal carbon mineralization rates (mmol C m^{-2} d^{-1}) estimated by model 10 (Table 4), assuming RQ=1.

A. Epilimnetic respiration estimated for chl a of 3 $\mu g\ l^{-1}$, using the regression presented in Fig. 8B. AHOD and sediment mineralization plotted as a function of mean depth.

Areal hypolimnetic respiration = 30 * log (mean depth) - 21, n=11, r^2=0.64, p<0.003

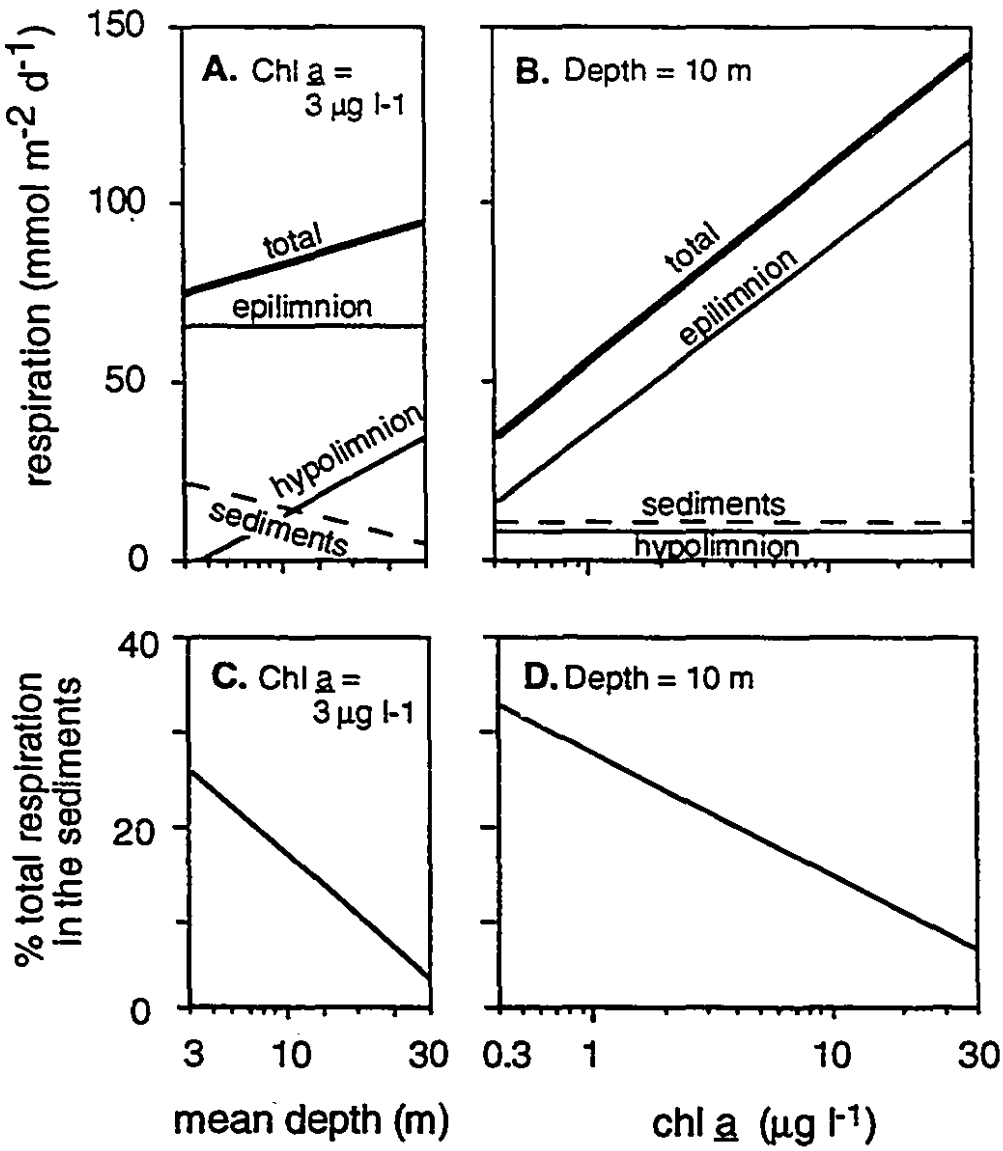
Areal sediment mineralization = -14 * log (mean depth) + 26, n=8, r^2=0.70, p<0.01

B. Hypolimnetic respiration and sediment mineralization predicted for a mean depth of 10 m (Fig. 8A), and epilimnetic respiration predicted from chl a.

Areal epilimnetic respiration = 50 * log (chl a) + 41, n=20, r^2=0.46, p<0.000

C. Sediment mineralization decreases from 26 to 5 % of the gross metabolism over the range of mean depth observed in the study lakes.

D. Sediment mineralization decreases from 33 to 8 % of gross respiration over the range in chl a reported in the study lakes.


A. Chl a = 3 µg l-1
B. Depth = 10 m
C. Chl a = 3 µg l-1
D. Depth = 10 m
respiration (mmol m-2 d-1)
% total respiration in the sediments
total
epilimnion
hypolimnion
sediments
150
100
50
0
40
20
0
3
10
30
0.3
1
10
30
mean depth (m)
chl a (µg l-1)

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Chapter 2.

An exploration of the utility of stable carbon isotope and carbon to nitrogen ratios of organic matter as measures of autochthonous inputs to lake sediments.

Abstract

Autochthonous organic material is believed to be the preferred substrate for heterotrophic bacteria. In order to assess the contribution of autochthonous and allochthonous material in sediments, I measured the carbon to nitrogen (C:N) and stable carbon isotope ($\delta^{13}C$) ratios of organic m: terial in the top centimeter of the sediments of 9 lakes in southern Quebec. At least 23% of the cores (n=13) have significant input of autochthonous material based on the $\delta^{13}C$ ratios. The littoral sand sites appear to accumulate allochthonous material while those shallow sites with macrophyte growth have more positive $\delta^{13}C$ values, reflecting the generally more positive $\delta^{13}C$ values of macrophytes. The average $\delta^{13}C$ value for the organic matter of the profundal sediments are more negative than that of the shallow sediments, and are not significantly different from allochthonous material. However, the C:N ratio of sediment organic matter is not coupled to variation in the contribution of autochthonous material within lakes as measured by the $\delta^{13}C$ ratios. Based on work in one lake, LaZerte (1983) argued that the $\delta^{13}C$ ratio of organic matter is a more sensitive measure of the autochthonous input than the C:N ratio. The present data support his interpretation within lakes, but it appears that the C:N ratio is a more useful measure of the relative contribution of autochthonous organic matter among lakes. The C:N ratio of the sediment organic matter is lower in lakes with greater phytoplankton biomass in the surface water whereas there is no significant correlation between the $\delta^{13}C$ ratio and lake trophy. Despite the different sensitivities of C:N and $\delta^{13}C$ ratios to variation in autochthonous content of the sediment within and among lakes, these tracers are too well correlated among the sources to serve as independent measures of source. A third independent measure of source is needed to quantitatively assess the contribution from autochthonous and allochthonous sources in lakes where macrophyte production is an important third source of sediment organic matter.

Introduction

Organic detritus in lakes is either composed of autochthonous material produced within the lake or allochthonous material brought into the lakes from their drainage basins. Autochthonous material, produced by phytoplankton, macrophytes and epiphytes, is considered the preferred substrate for heterotrophic bacteria (Wetzel 1983). Autocththonous material is generally characterized by lower nitrogen content than allochthonous terrestrial material and is also probably less refractory as it has not been exposed to degradation by the soil and riverine microbial communities. Thus autochthonous material should be higher quality substrate for bacteria, and sediments with greater autocthonous input could be expected to have a more metabolically active microbial community per unit quantity of organic matter.

The relative contribution of autochthonous material in sediments should be a function of the allochthonous and autochthonous loading as well as the exposure of sedimenting organic matter to microbial degradation. Exposure of organic matter to microbial activity within the lake not only reduces the absolute amount of material but also depletes the material of its more labile components (Wetzel 1983). Sedimenting organic matter composed of both allochthonous and autochthonous detritus should become enriched in allochthonous material over time as a result of microbial activity.

Sedimentation is spatially and temporally heterogeneous within lakes. Although deposition of particulate material on littoral sediments occurs throughout the year, the fine organic matter that was not immediately metabolized in the water column or at the sediment surface is resuspended during high energy periods and is ultimately transported to profundal sediments (Davis and Brubaker 1973; Davis 1973; Rowan et al. 1992). As a result, the profundal sediments are not only finer than littoral sediments (Rowan et al.

1992) but are also likely to contain a lower proportion of the more labile autochthonous material than littoral sediments.

Both C:N ratios and $\delta^{13}C$ ratios have been used as tracers of the organic matter source in aquatic systems (Nriagu 1982; Kemp et al. 1977; LaZerte 1983). Successful use of such tracers is dependent upon a clear distinction of the signature of the sources. The reported C:N ratio of phytoplankton ranges from 6 to 9 (Nriagu 1982; Kemp et al. 1977; LaZerte 1983; Martinova 1993). The C:N ratio of terrestrial material is much higher and more variable, with woody material having a much higher ratio than leaves. Nriagu (1982) report C:N ratios between 15 and 20 for allochthonous material in Ontario lakes. Soil litter in boreal forest has C:N ratio as high as 33, while stream litter has a lower range between 10.4 and 14.2 (Hecky et al. 1993). The isotope method is based on the fractionation of the carbon by primary producers that assimilate lighter CO_2 or HCO_3^- more readily than ^{13}C rich inorganic carbon (Farquhar et al. 1989). The stable carbon isotope ratio ($\delta^{13}C$) of primary producers is dependent on their physiology, the ambient temperature, and the size and the $\delta^{13}C$ value of the inorganic carbon pool. Terrestrial plants have $\delta^{13}C$ ratios ranging from -17 to -9 ‰ for C4 plants, and -32 to -20 ‰ for C3 plants (Boutton 1991). The latter dominate the drainage the largely forested drainage areas of the present study. An earlier study of the stable carbon isotope ratio of stream litter in similar catchments has shown the $\delta^{13}C$ value to be very stable at -28 +/- 1 ‰ (Schallenberg 1992) which is within the often quoted range of -30 to -26 ‰. Freshwater phytoplankton are more depleted in ^{13}C and are also more variable, ranging from -42 to -26 ‰ (Boutton 1991). The more variable carbon isotope composition of phytoplankton probably reflects greater variability in the $\delta^{13}C$ value and size of the inorganic carbon pool (Fry and Sherr 1984).

Both the $\delta^{13}C$ and C:N ratios of macrophytes are markedly different from those of phytoplankton and terrestrial material. The C:N molar ratio of macrophytes, ranging from

16 to 34, is variable and overlaps with the range in terrestrial material (Martinova 1993). Macrophytes do not fractionate carbon as strongly as phytoplankton and are often characterized by more positive values (Boutton 1992; France in press). They and their associated periphyton are more likely to experience carbon limitation than phytoplankton as a result of an increased boundary layer (Raven et al. 1982; Osmond et al.1981). The stable isotope ratio of macrophytes ranges from -50 to -10 ‰ (Keeley and Sandquist 1992), with a range for lakes between -32 and -12 ‰ (France in press). In order to assess the relative contributions of the three sources it is necessary to have two independent tracers (Peterson and Fry 1987). Both the stable carbon isotope and C:N ratios of the organic matter in the top centimeter of the littoral and profundal sediments of 9 lakes were measured in order to assess the relative contribution of autochthonous material to the sediments.

Methods

Fifty-five cores were taken from both littoral and profundal sediment of 9 lakes in the Laurentians and Eastern Townships of southern Quebec. Two to three replicate cores were analyzed from up to three habitats per lake, using 5 cm diameter PVC tube. The habitats were: (1) the profundal sediments of the lake or bay, (2) a shallow area with macrophyte growth and (3) a shallow area with coarse grained sediments and limited or no macrophyte growth. The deep sites were sampled with a gravity corer while cores were collected by SCUBA divers at the shallow sites. The top centimeter of the cores was removed using a vertical extruder. The sediment was then oven dried at 60 ^{o}C and prepared for stable isotope and C:N analysis on a Europa Scientific Tracermass mass spectrometer interfaced with a Roboprep-CN analyzer. Five to 10 ml of dried sediment was acidified with 10 ml of 2 to 3% phosphoric acid to remove carbonates from the sediments. The acid sediment mixture was shaken and left overnight to allow the acid to react. The samples were then oven dried at 60 ^{o}C and ground with mortar and pestle. Enough sediment to contain between 2 and 3 mg of organic matter, was packed into duplicate titanium capsules. The mean standard error of the $\delta^{13}C$ ratio of the duplicates, expressed as parts per thousand or per ml difference from PDB (Fry and Sherr 1984), is 0.26 ‰ (n=55) and the mean standard error of the C:N molar ratio was 0.40 (n=53). Five cores taken from the shallow sediments of Lake Bowker were removed from the analysis. These cores were from a shallow enclosed bay and had high $\delta^{13}C$ ratios, possibly resulting from incomplete removal of inorganic carbon.

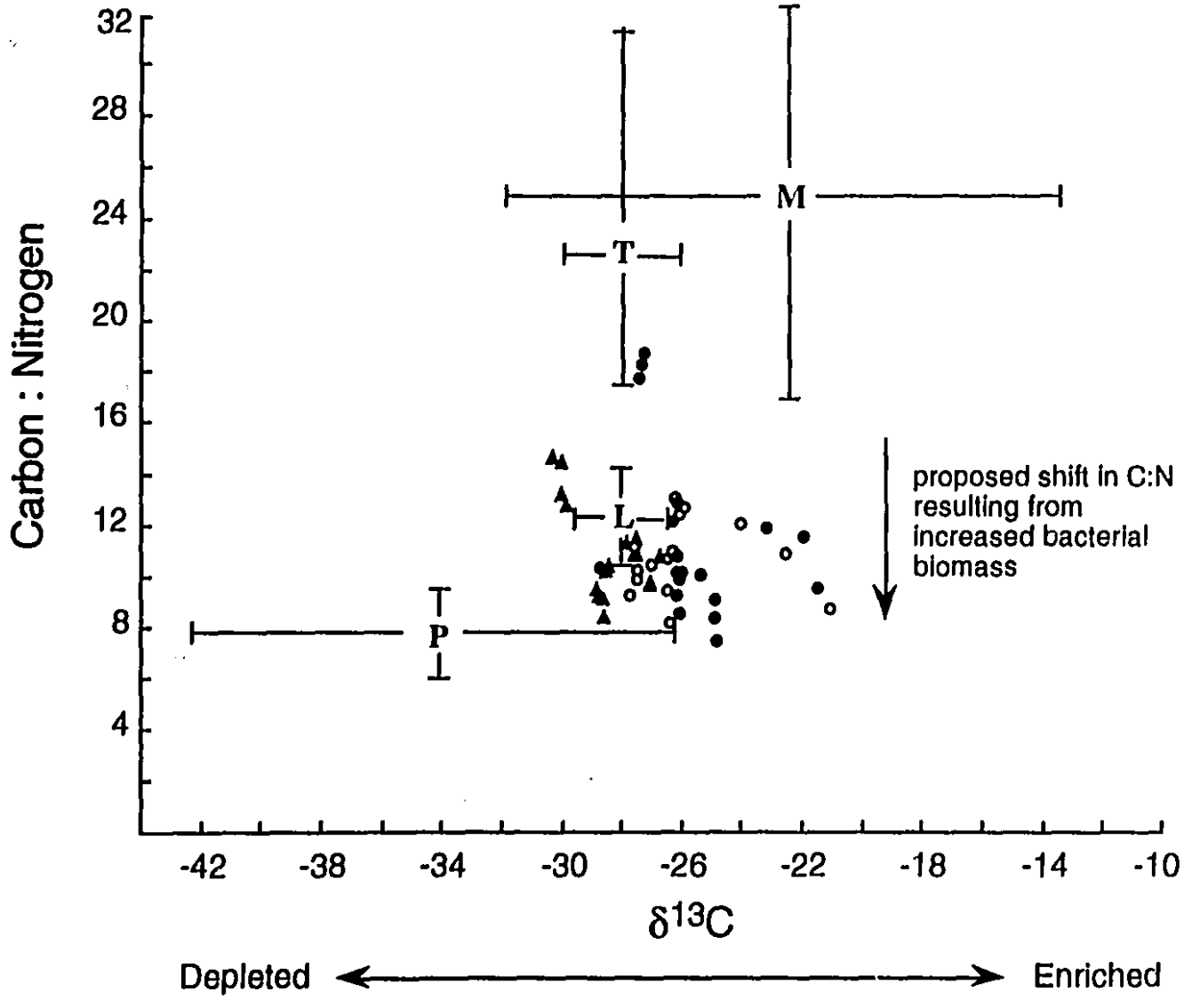
Results and Discussion

The range found in C:N and $\delta^{13}C$ ratios of the sediment organic material is similar to those reported previously (Schallenberg 1992; LaZerte 1983; Boutton 1991). The overall mean $\delta^{13}C$ (-26.6 ‰) is within the range of values reported for terrestrial material, suggesting that the dominant source of sediment organic material is allochthonous. However, 23% of the cores (n=13) have carbon isotope ratios beyond the -30 to -26 ‰ range (Fig. 1) for allochthonous input and therefore appear to contain a significant amount of autochthonously produced organic matter. In contrast, the C:N ratios of the sediment organic matter are almost entirely below the reported range for terrestrial material and stream litter, suggesting a greater input from phytoplankton. This discrepancy indicates that one or both of the ratios have been modified prior to deposition.

There is evidence that for modification of $\delta^{13}C$ of organic detritus resulting from differential degradation of organic compounds (Benner et al. 1987), but this process has been shown to have minimal effect on the $\delta^{13}C$ ratio of organic detritus with prolonged exposure to microbial degradation (Schwinghamer et al. 1983; Fenton and Ritz 1983). The $\delta^{13}C$ ratio of organic matter is more stable than the C:N ratio (LaZerte 1983; Thorton and McManus 1994). Enrichment of particulate organic matter upon exposure to decomposition has been documented in estuaries (Darnell 1967; Roman 1980). Bacteria have relatively low C:N ratios and with increasing bacterial biomass, particulate organic detritus becomes enriched in nitrogen. Bacterial biomass per gram dry weight is greater in the profundal sediments than in the littoral sediments, and as much as 20% of the organic carbon in lake sediments may be bacterial biomass (Schallenberg 1993). Assuming a C:N ratio of bacteria of 5 and a C:N ratio of the sediments of 10, bacterial nitrogen can account for 40% of the N in lake sediments.

Fig. 1. Plot of the C:N and stable carbon isotope ($\delta^{13}C$) ratios of organic matter in the surface sediment and the potential sources of this material. Ranges of the reported $\delta^{13}C$ ratios of macrophytes (M) (France in press), stream litter (Schallenberg 1992), phytoplankton (P) and terrestrial (T) material (Boutton 1991) are plotted against the reported ranges in C:N ratios for terrestrial and phytoplankton material (LaZerte 1983), stream litter (Hecky et al. 1993) and macrophytes (Martinova 1993). The symbols indentify the individual core collected from three habitats.

▲ profundal ● weedbed ○ sand sites.


Carbon : Nitrogen
32
28
24
20
16
12
8
4
M
T
L
P
proposed shift in C:N
resulting from
increased bacterial
biomass
-42
-38
-34
-30
-26
-22
-18
-14
-10
δ13C
Depleted
Enriched

There is a significant effect of lake and habitat on the $\delta^{13}C$ ratios of organic matter in the surficial sediments (Table 1a). The among lake differences in the sediment $\delta^{13}C$ ratio are associated with lake area (Table 2). The lower $\delta^{13}C$ values of the sediment organic matter in the smaller lakes suggests that there may be recycling of carbon. The signature of the DIC pool can vary by as much as 10 ‰, with values as low as -15 ‰ where there is input from the decomposition of terrestrial material (Fry and Sherr 1984). The lowest $\delta^{13}C$ values are observed in the profundal sediments of the shield lakes Cromwell and Croche. These two lakes have the smallest DIC pools and also receive high inputs of allochthonous material which may support organic matter mineralization in the water column. Therefore the DIC signature in these two lakes is more likely to be influenced by carbon recycling than in the hardwater lakes of the Eastern Townships.

The stable carbon isotope values of organic matter in the profundal, littoral sand and weedbed habitats are significantly different (Fig. 2). The $\delta^{13}C$ values of the sand and profundal habitats are not different from the terrestrial values, suggesting that the organic material in these sediments is for the most part of terrestrial origin. However, the profundal sites are more negative than the shallow habitats. LaZerte (1983) also observed more negative values in profundal sediments than in shallow inorganic sediments. He argued for a higher allochthonous input in the shallow sediments with less autochthonous material accumulating as a result of the increased energy of the shallow regions and transport of the fine particulate matter to the profundal region. The higher rate of organic matter mineralization in the warmer shallow sediments (chapter 1) may be equally effective at removing the more labile algal production. The $\delta^{13}C$ values of the organic matter in the weedbed sites was more positive than either that of the terrestrial material or phytoplankton apparently reflecting the input from the more positive macrophytes. Macrophyte produced organic matter appears to be a major source of organic detritus in weedbeds.

Table 1. An analysis of variance of the $\delta^{13}C$ and carbon to nitrogen ratio of the organic matter in the top centimeter of cores collected from 9 Quebec lakes in July and August of 1993. The three habitats sampled were: profundal, littoral weedbed, and littoral sandy. A Tukey test indicates a significant difference in the $\delta^{13}C$ among the all three habitats.

a) $\delta^{13}C$

Source	DF	Type III SS	MS	F Value	P
Model	20	86.11	4.31	28.05	0.0001
Lake	9	41.59	4.62	30.11	0.0001
Habitat	2	11.33	5.66	36.91	0.0001
Lake*Habitat	9	2.87	0.32	2.08	0.066
Error	32	4.45	0.15		
Total	49	90.56			

b) C:N

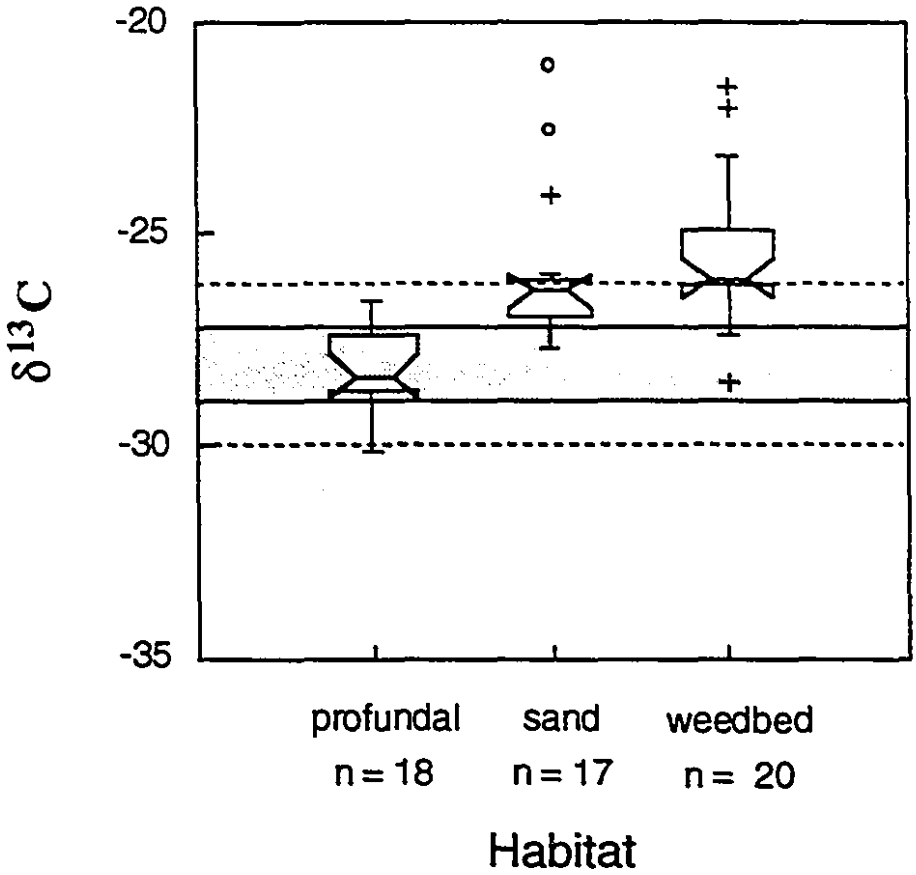
Source	DF	Type III SS	MS	F Value	P
Model	20	255.86	0.94	11.28	0.0001
Lake	9	75.06	8.34	8.64	0.0001
Habitat	2	3.86	1.93	2.00	0.15
Lake*Habitat	9	158.92	17.66	18.30	0.0001
Error	27	26.05	12.79		
Total	47	281.92			

Table 2. Pearson correlation matrix showing the significant correlations between the C:N and $\delta^{13}C$ of the organic matter in the top centimeter of individual cores and the environmental factors. The number of samples (n) is presented immediately below the correlation coefficients (r).

^{ns} p>0.05, * p<0.05, ** p<0.01, *** p<0.001.

	C:N (mol:mol)	CO_2+CH_4 (mmol $m^{-2}d^{-1}$)	site depth (m)	chl a (µg l^{-1})	lake area (km^2)	exposure (km^2)	Catchment area (km^2)
$\delta^{13}C$ (‰)	-0.24^{ns} 48	0.31* 48	-0.52*** 50	0.15^{ns} 36	0.46** 47	0.47*** 47	0.37* 47
C:N (mol:mol)		0.23^{ns} 46	-0.03^{ns} 48	-0.38* 39	-0.28^{ns} 45	-0.38** 45	-0.25^{ns} 45
CO_2+CH_4 (mmol $m^{-2}d^{-1}$)			-0.59*** 48	0.24^{ns} 45	0.30* 45	-0.14^{ns} 57	0.12^{ns} 57
site depth (m)				0.69*** 36	-0.23^{ns} 59	-0.24^{ns} 59	-0.34** 59
chl a (µg l^{-1})					0.30* 47	0.36* 47	0.49*** 47
lake area (km^2)						0.94*** 47	0.51*** 47
exposure (km^2)							0.54*** 47

Fig. 2. Box plot of stable carbon isotope ratio ($\delta^{13}C$) of the organic matter in the top centimeter of cores collected from southern Quebec lakes in the summer of 1993. The horizontal bars indicate the median, 25th and 75th percentiles, the o and + symbols indicate outside values and the notches represent he 95% confidence interval of the median. A Tukey test indicates significant differences among all three habitats. The two dashed lines represent a typical range in $\delta^{13}C$ value of terrestrial organic carbon (Boutton 1991), while the shaded area represents the value for terrestrial litter (Schallenberg 1992).


-20
-25
-30
-35
δ13C
profundal
n = 18
sand
n = 17
weedbed
n = 20
Habitat

There was a significant difference in the C:N ratios of the organic matter in the sediments among lakes and the ANOVA showed that the interaction of lake and habitat had a significant effect on the C:N ratios of the organic matter (Table 1b). In lakes with a greater standing stock of algae in the surface water the C:N ratio of the organic matter in the sediments is smaller (Table 2), suggesting that with increased phytoplankton production there is greater accumulation of autochthonous material in the sediment. In contrast, the sediment $\delta^{13}C$ ratios are not correlated with increased phytoplankton biomass probably because of the great among lake variability of $\delta^{13}C$ ratios of phytoplankton resulting from variability in the size and $\delta^{13}C$ ratios of dissolved inoragnic carbon pools among lakes. The among habitat variability highlighted by the $\delta^{13}C$ ratios is not apparent in the C:N ratios of the organic material. Modification of the C:N ratios of the sedimenting organic material within the water column and sediments may well mask the within lake differences indicated by the $\delta^{13}C$ ratios.

At first glance the smaller range of C:N ratios for the source materials would suggest that it could be a more powerful tracer of source than $\delta^{13}C$ ratios (Fig. 1). Indeed the C:N ratio appears to be a better measure of autochthonous contribution sediment among lakes. However, a large among lake variability in the $\delta^{13}C$ value of the phytoplankton could readily mask the differences in autochthonous contribution identified by the C:N ratio. Nonetheless, the $\delta^{13}C$ ratio appears to be a more sensitive measure of the autochthonous contribution within lakes than the C:N ratio, with the latter probably subject to greater modification in the water column and the sediments. Both LaZerte (1983), working in Lake Memphremagog, and Thorton and McManus (1994), working in the Tay Estuary, concluded that stable carbon isotope ratios provide a better tracer of organic matter than do C:N ratios.

Neither C:N nor $\delta^{13}C$ ratios alone are adequate to quantitatively assess the importance of allochthonous and autochthonous organic matter in systems where macrophytes are a significant source of organic detritus. In such systems two independent measures of source are needed to resolve the contribution from three sources. Although I have two distinct measures of source, the C:N and $\delta^{13}C$ ratios, the ratios of the sources are too variable and too well correlated (Fig. 1) to be used to quantitatively assess the contribution from the three sources.

The qualitative analysis of the C:N and $\delta^{13}C$ ratios suggests that there are significant differences in the contribution of autochthonous material to sediment organic matter both within and among lakes. The negative correlation between C:N ratio of the organic matter and phytoplankton biomass in the surface water is indicative of greater input of algal production to the surface sediment in more productive lakes, while variation in the $\delta^{13}C$ values of sediment organic matter inidicates within lake variability of autocthonous input. The weedbed sediments with their more positive $\delta^{13}C$ values appear to receive a significant proportion of organic matter from autochthonous production. The difference between the sand and profundal sediments further suggests a greater accumulation of phytoplankton material in the profundal sediments than in the littoral sediments as was also argued by LaZerte (1983). Unfortunately, the lack of $\delta^{13}C$ values of the phytoplankton in the study lakes does not allow a rigorous test of this hypothesis.

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Thesis Conclusions

Littoral sediments have been for the most part ignored by microbiologists, despite the high variability in the physical characteristics of the sediments in the littoral zone and the higher temperature of the overlying water. The present analysis shows that the areal rates of organic matter mineralization are higher and more variable in littoral than in profundal sediments. Mineralization rates in shallow sediments are on average 3 to 4 fold higher than profundal sediments, and at least 50% of the organic matter mineralization in the sediments of the lakes of this study occurs in the sediments overlain by epilimnetic water.

Variability in organic matter mineralization rates among the sand, weedbed, and profundal habitats is greater than the variability among lakes, with the strongest individual predictor of areal mineralization rate being the depth of the overlying water column. The high rate of organic matter mineralization in shallow sediments is at least in part due to the warmer temperature of the overlying water. There may also be differences with depth in the quality of sediment organic matter as substrate for the microbial communities.

Quality of detritus as substrate for bacteria is argued to be a function of both the source and the refractory nature of the organic material (Wetzel 1983). The analysis of C:N and $\delta^{13}C$ ratios of the organic matter in the surface sediment suggests that there is variability in the contribution of autocthonous detritus to sediment organic matter both within and among lakes. However, neither of these measures nor the algal biomass in the surface water were correlated with the mineralization rate or the residuals of the regression between mineralization rate and site depth, indicating that the sediment microbial community is not directly limited by algal production in the surface water.

Organic material in the profundal sediment, irrespective of source, may be of lower quality because of greater exposure to microbial degradation in the water column and in the littoral sediment prior to transport to the profundal zone. The lake specific parameters which were most strongly correlated with the areal rate of mineralization was the catchment area to lake area ratio and water residence time. I have interpreted these variables, in accordance with the literature, as surrogates for organic matter retention and/or quality. However, it is possible that site depth and the flushing rate of the lake affect the microbial community via effects on oxidant diffusion and/or sediment stability. A more direct assessment of organic matter quality could at least assess the first of these hypothesis.

It is difficult to assess substrate quality by chemical analysis. Bioassay techniques have been successfully employed to assess DOC qualtity in the water column (Tranvik 1990) and rates of degradative processes based on sediment slurries have been used to assess the reactivity of sediment organic matter (Hargrave 1972; Kelly and Chynoweth 1981; Burdidge 1991). Hargrave (1972) observed higher rates O_2 consumption per unit organic matter in sediments with smaller particle size, and both Kelly and Chynoweth (1981) and Burdidge (1991) working on lakes and estuarine sediment respectively, observed variability in the reactivity of organic matter among sites, and a decrease in reactivity with depth in sediment cores. Similar techniques could be used to compare the lability of organic material in profundal and littoral sediments.

Not surprisingly, given the correlation of sediment mineralization rates with site depth, both total mineralization and mean areal mineralization in the sediments is a function of lake morphometry. My work supports and extends the conceptual model of Charlton (1980). Not only is the mean areal rate of organic matter mineralization higher in shallow lakes, but the smaller volume of these lakes results in a greater importance of

sediments relative to water column mineralization. However, respiration in epilimnetic water dominates lake respiration because of the relatively large planktonic biomass, and therefore organic matter mineralization in the sediments is a smaller proportion of the total respiration than is indicated by Charlton's model.

The relative importance of the sediments in lake respiration is a function of both the algal biomass in the surface waters and lake morphometry. The sediments play a smaller role in metabolism in more eutrophic lakes than in oligotrophic lakes of the same size and shape (mean depth), and a greater role in shallow lakes than in deep lakes of a particular trophic status. Shallow lakes, dominated by their littoral zones, are much more common than deep lakes (Wetzel 1990), and future work on sediment processes might profitably focus on the littoral sediments.

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Appendix A

Appendix A includes the data collected from the individual sediment cores.

Three lakes, Lac Croche, Lac Cromwell and Lac Achigan are on the Canadian shield. The six other lakes are in the Eastern Townships of Quebec.

The sites are: **p** profundal

s littoral sand

wb littoral weedbed.

For each site there were up to three replicates (Rep.).

Depth refers to the thickness of the water column overlying the site.

The methods for determining water content and organic matter content in the top centimeter of the core are given in chapter 1.

The remineralization rates (DIC + CH_4 release, mmol $m^{-2}d^{-1}$) were determined in intact cores as described in chapter 1.

Lake	Site	Month	Rep.	Incubation time	Incubation temp.	Depth	Water content	Organic matter	DIC + CH_4 release
				days	^oC	m	% fresh weight	% dry weight	mmol m^{-2} d^{-1}
Achigan									
	p	6	1	4	4	12.0	0.90	0.25	7.66
			2	4	4	12.0	0.94	0.23	2.81
			3	4	4	12.0	0.89	0.23	7.05
		7	1	3	8	12.0	0.89	0.22	-0.75
			2	3	8	12.0	0.91	0.23	2.15
			3	3	8	12.0	0.91	0.22	1.60
		8	1	4	8	16.0	0.89	0.23	5.91
			2	4	8	16.0	0.89	0.23	9.45
			3	4	8	16.0	0.87	0.22	5.06
		10	1	4	8	17.5	0.91	0.23	6.56
			2	4	8	17.5	0.91	0.21	7.19
	s	6	1	4	20	3.1	0.65	0.07	19.17
			2	4	20	3.1	0.71	0.08	20.69
			3	4	20	3.1	0.69	0.06	16.36
		7	1	4	24	3.0	0.73	0.07	-7.43
			2	4	24	3.0	0.72	0.07	31.34
			3	4	24	3.0	0.70	0.07	30.43
		8	1	4	24	3.8	0.71	0.08	14.98
			2	4	24	3.1	0.68	0.07	18.42
			3	4	24	2.8	0.64	0.06	30.62
		10	1	4	8	3.0	0.73	0.06	13.27
			2	4	8	3.0	0.71	0.06	12.78
			3	4	8	3.0	0.45	0.02	12.47
	wb	6	1	4	20	1.9	0.56	0.04	43.08
			2	4	20	1.9	0.60	0.05	25.10
			3	4	20	1.9	0.53	0.03	34.54
		7	1	4	24	3.0	0.71	0.07	22.04
			2	4	24	3.0	0.71	0.06	22.34
			3	4	24	3.0	0.73	0.07	27.12
		8	1	4	24	2.8	0.73	0.07	27.30
			2	4	24	2.8	0.77	0.08	30.08
			3	4	24	2.2	0.63	0.05	30.74
		10	1	4	8	4.0	0.80	0.08	6.09
			2	4	8	4.6	0.79	0.08	7.75
			3	4	8	4.6	0.79	0.08	14.03
Bowker									
	p	6	1	4	4	32.0	0.95	0.20	17.61
		7	1	4	10	33.5	0.89	0.20	9.59
			2	4	10	35.0	0.89	0.19	12.92
			3	4	10	35.0	0.91	0.19	5.06
		8	1	4	4	33.0	0.85	0.18	-0.09
			2	4	4	32.0	0.83	0.23	-1.89
			3	4	4	30.0	0.82	0.18	3.11
	s	6	1	4	20	1.0	0.66	0.06	15.26

			2	4	20	1.0	0.74	0.06	16.15
			3	4	20	1.0	0.71	0.06	23.90
		7	1	4	20	1.0	.	0.03	12.84
			2	4	20	1.0	.	0.02	-16.31
			3	4	20	1.2	.	0.02	111.69
		8	1	4	24	1.5	0.62	0.04	28.06
			2	4	24	1.5	0.44	0.02	34.40
			3	4	24	1.5	0.44	0.04	29.36
	wb	6	1	4	20	1.0	0.86	0.12	22.01
			2	4	20	1.0	0.88	0.14	17.60
			3	4	20	1.0	0.81	0.10	19.51
		7	1	4	20	1.0	.	0.12	69.89
			2	4	20	1.0	.	0.14	39.76
			3	4	20	1.0	.		40.40
		8	1	4	24	1.0	0.88	0.25	17.74
			2	4	24	1.0	0.91	0.19	23.33
			3	4	24	1.0	0.93	0.21	25.24
Brome									
	p	8	1	4	20	6.2	0.42	0.03	11.83
			2	4	20	6.2	0.38	0.02	11.15
			3	4	20	6.2	0.38	0.02	9.89
	s	7	1	4	24	1.8	0.26	0.01	.
			2	4	24	1.8	0.23	0.01	14.18
			3	4	24	1.8	0.26	0.01	49.94
		8	1	4	24	1.2	0.36	0.02	33.88
			2	4	24	1.2	0.36	0.02	24.27
			3	4	24	1.2	0.35	0.02	31.23
	wb	7	1	4	24	1.2	0.49	0.03	37.22
			2	4	24	1.8	0.51	0.03	27.32
			3	4	24	2.0	0.82	0.07	47.08
		8	1	4	24	1.9	.	.	10.05
			2	4	24	1.7	.	.	17.14
			3	4	24	1.7	0.63	0.05	36.21
		10	1	4	8	1.2	0.83	0.09	8.39
			2	4	8	1.2	0.77	0.10	7.59
			3	4	8	1.2	0.67	0.08	7.18
Croche									
	p	6	1	4	4	9.0	0.98	0.48	6.73
			2	4	4	9.0	0.97	0.47	2.87
			3	4	4	9.0	0.97	0.48	10.34
		7	1	4	4	8.0	.	0.46	4.39
			2	4	4	8.0	.	0.45	6.66
			3	4	4	8.0	.	0.47	5.93
		8	1	4	8	8.5	0.96	0.44	.
			2	4	8	8.5	0.96	0.45	.
		10	1	4	8	7.0	0.97	0.46	3.31
			2	4	8	7.0	0.97	0.46	5.96
			3	4	8	7.0	0.97	0.46	6.66
Cromwell									
	p	6	1	4	4	9.0	0.99	0.52	1.21
			2	4	4	9.0	0.98	0.53	3.04
			3	4	4	9.0	0.98	0.53	3.02

		7	1	4	4	9.5	.	.	3.45
			2	4	4	9.5	.	0.56	4.03
			3	4	4	9.5	.	0.55	-5.74
		8	1	4	8	9.0	.	.	4.12
			2	4	8	9.0	.	.	.
			3	4	8	9.0	.	.	10.75
		10	1	4	8	9.0	.	.	7.72
			2	4	8	9.0	.	.	4.23
			3	4	8	9.0	.	.	.
	wb	6	1	4	10	2.1	0.90	0.60	16.40
			2	4	10	2.1	.	.	28.80
			3	4	10	3.0	0.85	.	42.46
		7	1	4	8	2.0	0.99	0.61	17.65
			2	4	8	2.0	0.98	0.62	16.26
			3	4	8	3.0	0.97	0.59	20.96
		8	1	4	20	1.4	0.94	0.54	25.87
			3	4	20	1.4	.	.	29.30
		10	1	4	8	2.7	0.98	0.60	-1.04
			2	4	8	2.7	0.98	0.57	1.55
			3	4	8	2.7	0.97	0.55	.
Hertel									
	p	6	1	4	16	8.0	0.92	0.38	19.22
			2	4	16	8.0	0.93	0.39	14.06
			3	4	16	8.0	0.96	0.32	14.46
		7	1	4	8	7.5	0.97	0.37	7.42
			2	4	8	7.5	0.96	0.36	-9.47
			3	4	8	7.5	.	.	2.97
		8	1	4	16	8.0	0.92	0.53	2.56
			2	4	16	8.0	0.96	0.37	14.13
			3	4	16	8.0	.	.	10.95
	s	7	1	4	20	1.2	.	.	15.32
			2	4	20	1.2	.	0.01	28.40
			3	4	20	1.2	.	0.01	-8.36
		8	1	4	20	1.7	0.27	0.02	4.57
			2	4	20	3.8	0.24	0.04	4.77
			3	4	20	1.7	0.29	0.03	34.07
	wb	6	1	4	16	1.1	0.94	0.29	42.96
			2	4	16	1.1	0.97	0.32	13.97
			3	4	16	1.1	0.94	0.28	26.60
		7	1	4	20	5.0	.	0.31	33.01
			2	4	20	5.0	.	0.27	27.51
			3	4	20	5.0	.	0.30	66.05
		8	1	4	20	1.0	0.89	0.19	29.35
			2	4	20	1.0	0.94	0.33	23.93
			3	4	20	1.0	0.94	0.41	19.89
Magog									
	p	6	1	4	12	10.0	0.91	0.18	8.44
			2	4	12	10.0	0.93	0.18	23.48
			3	4	12	10.0	0.91	0.18	7.81
		7	1	4	20	5.5	.	0.15	-2.28
			2	4	20	5.5	.	0.16	.
			3	4	20	5.5	.	0.15	7.29
		8	1	4	20	10.0	0.89	0.16	1.87

		2	4	20	3.7	0.54	0.13	-19.53
		3	4	20	3.7	0.86	0.14	7.71
	10	1	3	12	4.9	0.91	0.17	7.36
		2	3	12	4.9	0.92	0.17	6.89
		3	3	12	4.9	0.97	0.17	-1.10
s	6	1	4	22	1.2	0.26	0.03	26.30
		2	4	22	1.2	0.36	0.03	41.47
		3	4	22	1.2	0.49	0.06	17.44
	7	1	4	24	1.0	0.28	0.02	11.56
		2	4	24	0.8	0.35	0.02	16.08
		3	4	24	0.8	0.25	0.03	-45.33
	8	1	4	20	0.6	.	.	3.74
		2	4	20	0.8	0.39	0.04	12.92
		3	4	20	0.9	0.39	0.10	13.45
	10	1	3	12	0.9	0.19	0.02	-7.93
		2	3	12	0.9	0.29	0.03	10.06
		3	3	12	0.9	0.34	0.04	70.18
wb	6	1	4	22	1.2	0.60	0.07	24.83
		2	4	22	1.2	0.71	0.10	34.45
		3	4	22	1.2	0.60	0.06	27.11
	7	1	4	24	1.5	0.81	0.11	-49.59
		2	4	24	1.5	0.79	0.10	34.49
		3	4	24	1.5	0.79	0.13	16.78
	8	1	4	20	1.5	0.88	0.16	31.73
		2	4	20	1.5	0.89	0.16	15.26
		3	4	20	1.5	0.90	0.16	15.45
	10	1	3	12	1.7	0.84	0.14	27.07
		2	3	12	1.7	0.69	0.13	39.75
		3	3	12	1.7	0.86	0.14	24.08
Memphremagog								
Quinn Bay								
p	7	1	3	16	12.0	0.92	0.22	-9.34
		2	3	16	12.0	0.94	0.23	8.69
		3	3	16	12.0	0.92	0.23	6.89
		4	3	16	12.0	.	.	19.40
Green Bay								
p	8	1	4	4	25.5	0.92	0.21	6.41
		2	4	4	25.5	0.91	0.21	.
s	7	1	4	20	6.0	.	0.04	-12.84
		2	4	20	1.8	.	0.18	35.68
		3	4	20	3.0	.	0.27	52.22
	8	1	4	20	1.9	0.78	0.16	24.58
		2	4	20	4.7	0.33	0.04	13.04
		3	4	20	4.7	0.32	0.03	6.85
	10	2	4	8	1.8	0.27	0.02	3.04
		3	4	8	1.8	0.41	0.05	23.47
		3	4	8	2.4	0.52	0.06	4.31
wb	6	1	4	12	1.4	0.72	0.16	23.13
		2	4	12	1.4	0.66	0.16	32.69
		3	4	12	1.4	0.77	0.17	.
		4	4	12	1.4	0.88	0.17	48.85
	7	1	4	20	1.2	.	0.19	55.50
		2	4	20	2.0	.	0.15	66.41

		3	4	20	3.0	.	0.21	58.92
	8	1	4	20	1.9	0.77	0.12	8.73
		2	4	20	1.2	0.85	0.19	74.63
		3	4	20	1.9	0.82	0.19	22.14
	10	1	4	8	1.8	0.87	0.15	7.65
		2	4	8	1.8	0.90	0.19	7.42
		3	4	8	1.8	0.90	0.20	11.83
Waterloo								
p	6	1	4	16	4.0	0.93	0.32	9.89
		2	4	16	4.0	0.96	0.32	10.28
		3	4	16	4.0	0.95	0.41	9.25
	7	1	4	20	5.0	.	0.29	.
		2	4	20	5.0	.	0.27	12.25
		3	4	20	5.0	.	0.28	23.73
	8	1	4	20	4.0	0.93	0.31	20.64
		2	4	20	4.0	0.90	0.51	14.40
		3	4	20	4.0	0.92	0.42	19.15
	10	1	3	12	4.6	0.84	0.32	3.91
		2	3	12	4.6	0.85	0.31	-4.03
		3	3	12	4.6	0.95	0.32	8.97
s	6	1	4	16	1.0	0.22	0.01	15.44
		2	4	16	1.0	0.21	0.01	.
		3	4	16	1.0	0.21	0.01	11.16
	7	1	4	24	1.2	0.24	0.01	36.40
		2	4	24	1.2	0.27	0.01	27.37
		3	4	24	1.5	0.24	0.01	27.66
	8	1	4	20	1.0	0.39	0.02	30.19
		2	4	20	1.0	0.36	0.02	25.80
		3	4	20	1.0	0.36	0.02	40.18
	10	1	3	8	1.5	0.46	0.02	24.39
		2	3	8	1.7	0.38	0.02	4.39
		3	3	8	1.7	0.33	0.02	-6.16
wb	6	1	4	16	1.2	0.93	0.31	21.38
		2	4	16	1.2	0.85	0.27	.
		3	4	16	1.2	0.61	0.08	-10.01
	7	1	4	24	1.2	0.90	0.30	36.25
		2	4	24	1.2	0.90	0.30	-23.50
		3	4	24	1.2	0.90	0.29	9.63
	8	1	4	20	1.2	0.87	0.33	41.04
		2	4	20	1.9	0.82	0.27	41.73
		3	4	20	1.9	0.79	0.21	64.81
	10	1	3	8	1.2	0.84	0.29	-4.48
		2	3	8	1.2	0.90	0.25	-44.71
		3	3	8	1.2	0.91	0.28	12.45

Appendix B

Appendix B includes the lake and site characteristics.

Three lakes, Lac Croche, Lac Cromwell and Lac Achigan are on the Canadian shield. The six other lakes are in the Eastern Townships of Quebec.

The sites are:

p	profundal
s	littoral sand
wb	littoral weedbed.

For each site there were up to three replicates (Rep.).

Chl a is the concentration in surface water and is the mean of three replicates.

Mixing depth is defined as the depth of maximum temperature change.

*	temperature profile indicates the water column to be completely mixed
**	water column assumed to be completely mixed
na	temperature profiles not available

Site exposure was determined from bathymetric maps using planimetry.

Lake	month	chl a	mixing depth	site	exposure
		$\mu g\ l^{-1}$	m		km^2
Achigan	6	1.99	8	p	3.37
				s	2.01
				wb	2.01
	7	1.87	8	p	3.37
				s	2.01
				wb	2.01
	8	1.77	na	p	3.37
				s	2.01
				wb	2.01
	10	2.23	25*	p	3.37
				s	2.01
				wb	2.01
Bowker	6	0.77	6	p	1.86
			6	s	0.40
			6	wb	0.40
	7	0.60	5	p	1.86
				s	0.40
				wb	0.40
	8	1.25	7	p	1.86
				s	0.40
				wb	0.40
Brome	7	4.97	7	s	12.77
				wb	5.57
	8	11.39	7	p	12.77
				s	12.77
				wb	5.57
	10	7.37	11.5**	wb	5.57
Croche	6	2.48	3	p	0.03
	7	1.45	3	p	0.03
	8	2.64	2	p	0.03
	10	3.92	10**	p	0.03
Cromwell	6	5.71	2	p	0.09
				wb	0.09
	7	2.92	2	p	0.09
				wb	0.09
	8	9.27	2	p	0.09
				wb	0.09
	10	3.93	9.5**	p	0.09
				wb	0.09
Hertel	6	5.43	9	p	0.32
				wb	0.29
	7	3.70	3	p	0.32
				s	0.29
				wb	0.29
	8	.	na	p	0.32
				s	0.29
				wb	0.29
Magog	6	5.53	9	p	7.92

				s	5.91
				wb	5.91
	7	5.00	9	p	7.92
				s	5.91
				wb	5.91
	8	9.82	9	p	7.92
				s	7.92
				wb	7.92
	10	4.66	17.5**	s	6.92
				wb	5.91
Memphremagog					
Green Bay	6	4.08	na	wb	2.40
				s	2.40
				wb	2.40
	8	3.40	na	p	2.40
				s	2.40
				wb	2.40
	10	3.65	na	s	2.40
				wb	2.40
Waterloo	6	7.21	5	p	1.50
				s	1.39
				wb	0.54
	7	14.52	5	p	1.50
				s	1.36
				wb	0.54
	8	.	4.9*	p	1.50
				s	1.39
				wb	0.54
	10	11.64	4.9*	p	1.50
				s	1.39
				wb	0.54

Appendix C

Appendix C includes the C:N and the stable carbon isotope ($\delta^{13}C$) ratios of organic matter in surface sediment.

Three lakes, Lac Croche, Lac Cromwell and Lac Achigan are on the Canadian shield. The six other lakes are in the Eastern Townships of Quebec.

The sites are; **p** profundal
s littoral sand
wb littoral weedbed.

For each site there were up to three replicates (Rep.).

Depth refers to the thickness of the water column overlying the site.

C:N and $\delta^{13}C$ ratios of the organic matter in the top centimeter of the sediment are the means of duplicates prepared as described in chapter 2.

Lake	Site	Month	Rep.	depth m	C:N	$\delta^{13}C$ ‰
Achigan	p	7	1	12.0	10.73	-27.40
	s	8	1	3.8	10.84	-26.30
	s	8	2	3.1	9.42	-26.42
	wb	8	1	2.8	10.14	-26.16
	wb	8	2	2.8	10.12	-25.97
	wb	8	3	2.2	8.48	-26.05
Bowker	p	7	1	33.5	10.64	-26.64
	p	7	2	35.0	11.30	-27.36
	p	7	3	35.0	11.11	-27.72
	s	8	1	1.5	10.84	-22.56
	s	8	2	1.5	8.73	-21.06
	wb	8	1	1.0	11.83	-23.18
	wb	8	2	1.0	11.48	-21.93
	wb	8	3	1.0	9.54	-21.50
Brome	s	8	1	1.2	8.15	-26.34
	s	8	2	1.2	.	-26.47
	s	8	3	1.2	10.71	-26.42
	wb	8	3	1.7	8.34	-24.92
Croche	p	7	1	8.0	14.30	-29.90
	p	7	2	8.0	14.46	-30.16
Cromwell	p	7	2	9.5	12.62	-29.75
	p	7	3	9.5	13.07	-29.87
	wb	8	1	1.4	10.36	-28.68
Hertel	p	7	1	7.5	9.58	-26.90
	p	7	2	7.5	10.70	-27.48
	s	8	1	1.7	12.45	-26.06
	s	8	2	3.8	12.06	-24.04
	wb	8	1	1.0	10.07	-25.37
	wb	8	2	1.0	9.08	-24.90
	wb	8	3	1.0	7.44	-24.82
Magog	p	7	2	5.5	9.51	-26.89
	p	7	3	5.5	.	-27.25
	s	8	2	0.8	12.69	-25.94
	s	8	3	0.9	10.96	-26.28
	wb	8	1	1.5	9.92	-26.05
	wb	8	2	1.5	9.90	-26.07
	wb	8	3	1.5	9.26	-26.14
Memphremagog Green Bay	s	8	1	1.9	13.07	-26.23
	s	8	2	4.7	9.29	-27.72
	s	8	3	4.7	10.39	-27.02
	wb	8	1	1.9	10.82	-26.13
	wb	8	2	1.2	12.13	-26.31
	wb	8	3	1.9	12.85	-26.14
Quinn Bay	p	7	1	12.0	10.28	-28.32
	p	7	2	12.0	9.01	-28.47
	p	7	3	12.0	9.32	-28.74
Waterloo	p	7	1	5.0	10.05	-28.44
	p	7	2	5.0	8.24	-28.46

p	7	3	5.0	9.08	-28.61
s	8	1	1.0	10.26	-27.50
s	8	2	1.0	11.18	-27.54
s	8	3	1.0	9.85	-27.45
wb	8	1	1.2	18.74	-27.22
wb	8	2	1.9	18.31	-27.35
wb	8	3	1.9	17.76	-27.40

Appendix D

Appendix D includes hypsographic data used in the depth integrated estimate of organic matter mineralization.

Depth is the depth of the overlying water column in meters.

Area at depth is the surface area between the depth and the next depth contour.

DIC and CH_4 release (mmol m^{-2} d^{-1}) is estimated from model 10 (Table 4, Chapter 1).

The Σ DIC + CH_4 release is the sum of the release of the product of the areal mineralization rate at depth times the area at depth (mol $summer^{-1}$).

* indicates the mean epilimnetic depth of the lake for June, July and August, and the corresponding Σ DIC + CH_4 is the flux (mol $summer^{-1}$) of carbon from the sediments overlain by epilimnetic water.

depth	area at depth	DIC + CH_4 release		Σ DIC + CH_4 release
	m^2	mmol m^{-2} d^{-1}	mmol d^{-1}	mol $summer^{-1}$
Achigan				
0	1.30E+05	52.56	6.85E+06	
1	1.48E+05	26.60	3.94E+06	
2	1.64E+05	19.38	3.18E+06	
3	1.79E+05	15.73	2.81E+06	
4	1.92E+05	13.46	2.58E+06	
5	2.03E+05	11.88	2.42E+06	
6	2.13E+05	10.72	2.28E+06	
7	2.21E+05	9.81	2.17E+06	
8*	2.28E+05	9.07	2.07E+06	2.5E+06
9	2.33E+05	8.47	1.97E+06	
10	2.36E+05	7.96	1.88E+06	
11	2.38E+05	7.52	1.79E+06	
12	2.38E+05	7.14	1.70E+06	
13	2.37E+05	6.81	1.61E+06	
14	2.34E+05	6.52	1.52E+06	
15	2.29E+05	6.25	1.43E+06	
16	2.23E+05	6.01	1.34E+06	
17	2.15E+05	5.80	1.24E+06	
18	2.05E+05	5.60	1.15E+06	
19	1.94E+05	5.42	1.05E+06	
20	1.81E+05	5.26	9.52E+05	
21	1.67E+05	5.10	8.51E+05	
22	1.51E+05	4.96	7.48E+05	
23	1.33E+05	4.83	6.44E+05	
24	9.92E+04	4.71	4.67E+05	4.4E+06
Bowker				
0	1.38E+05	28.50	3.93E+06	
2.95	6.90E+04	14.52	1.00E+06	
5.9*	7.03E+04	10.59	7.45E+05	1.6E+05
8.85	9.91E+04	8.60	8.53E+05	
11.8	9.95E+04	7.37	7.33E+05	
14.75	8.58E+04	6.51	5.58E+05	
17.7	1.18E+05	5.87	6.89E+05	
23.6	1.58E+05	4.97	7.86E+05	
29.5	2.39E+05	4.36	1.04E+06	
35.4	2.36E+04	3.91	9.24E+04	9.4E+05
Brome				
0	7.76E+05	53.78	4.17E+07	
1	1.03E+06	27.22	2.80E+07	
2	1.23E+06	19.83	2.44E+07	
3	1.38E+06	16.09	2.21E+07	
4	1.47E+06	13.77	2.02E+07	
5	1.51E+06	12.16	1.83E+07	

6	1.49E+06	10.96	1.64E+07	
7*	1.43E+06	10.03	1.43E+07	1.7E+07
8	1.31E+06	9.28	1.21E+07	
9	1.13E+06	8.67	9.80E+06	
10	9.03E+05	8.14	7.35E+06	
11	4.55E+05	7.70	3.50E+06	2.0E+07
Croche				
0	2.28E+04	56.19	1.28E+06	
1	2.19E+04	28.43	6.22E+05	
2	2.10E+04	20.71	4.35E+05	
3*	2.01E+04	16.81	3.38E+05	2.4E+05
4	1.92E+04	14.39	2.77E+05	
5	1.84E+04	12.71	2.33E+05	
6	1.75E+04	11.45	2.00E+05	
7	1.66E+04	10.48	1.74E+05	
8	1.57E+04	9.70	1.52E+05	
9	1.35E+04	9.05	1.22E+05	3.5E+05
Cromwell				
0	2.13E+04	39.59	8.44E+05	
1	1.59E+04	20.04	3.19E+05	
2*	1.15E+04	14.60	1.68E+05	1.2E+05
3	7.97E+03	11.85	9.44E+04	
4	5.38E+03	10.14	5.45E+04	
5	3.72E+03	8.95	3.33E+04	
6	3.00E+03	8.07	2.42E+04	
7	3.21E+03	7.39	2.37E+04	
8	4.35E+03	6.84	2.97E+04	
9	4.80E+03	6.38	3.06E+04	1.5E+05
Hertel				
0	1.02E+05	35.24	3.58E+06	
2	4.52E+04	17.83	8.06E+05	
4	5.31E+04	12.99	6.90E+05	
6*	8.38E+04	10.54	8.83E+05	5.4E+05
8	6.24E+03	9.02	5.63E+04	5.4E+05
Magog				
0	7.12E+05	22.73	1.62E+07	
1	6.90E+05	11.50	7.94E+06	
2	6.66E+05	8.38	5.58E+06	
3	6.42E+05	6.80	4.37E+06	
4	6.18E+05	5.82	3.60E+06	
5	5.95E+05	5.14	3.06E+06	
6	5.71E+05	4.63	2.65E+06	
7	5.47E+05	4.24	2.32E+06	
8	5.24E+05	3.92	2.06E+06	
9*	5.00E+05	3.66	1.83E+06	4.5E+06
10	4.77E+05	3.44	1.64E+06	
11	4.53E+05	3.25	1.47E+06	
12	4.29E+05	3.09	1.33E+06	

13	4.06E+05	2.95	1.20E+06	
14	3.82E+05	2.82	1.08E+06	
15	3.58E+05	2.70	9.69E+05	
16	3.35E+05	2.60	8.71E+05	
17	2.78E+05	2.51	6.98E+05	5.3E+06
Waterloo				
0	2.41E+05	40.82	9.84E+06	
1.52	4.66E+05	20.66	9.63E+06	
3.04	4.06E+05	15.03	6.10E+06	
4.57*	3.87E+05	12.20	4.72E+06	2.7E+06