Biogeochemistry **24**: 145–172, 1994.

The organic carbon budget of a shallow Arctic tundra lake on the Tuktoyaktuk Peninsula, N.W.T., Canada

Arctic lake carbon budget

P. S. RAMLAL[1,*], R. H. HESSLEIN[2], R. E. HECKY[2], E. J. FEE[2], J. W. M. RUDD[2] & S. J. GUILDFORD[2]

[1] *Department of Microbiology, University of Manitoba, Winnipeg, Manitoba, Canada R3T 2N2;*
[2] *Freshwater Institute, Central and Arctic Region, Department of Fisheries and Oceans, 501 University Crescent, Winnipeg, Manitoba, Canada R3T 2N6*
* *Present address: 605 Townsend Avenue, Winnipeg, Canada MB R3T 2V3*

Received 6 October 1993; accepted 23 February 1994

Key words: Arctic lake, carbon cycle, organic carbon budget

Abstract. The organic carbon cycle of a shallow, tundra lake (mean depth 1.45 m) was followed for 5 weeks of the open water period by examining CO_2 fluxes through benthic respiration and anaerobic decomposition, photosynthesis of benthic and phytoplankton communities and gas exchange at the air-water interface. Total photosynthesis (as consumption of carbon dioxide) was 37.5 mmole C m^{-2} d^{-1}, 83% of which was benthic and macrophytic. By direct measurement benthic respiration exceeded benthic photosynthesis by 6.6 mmole C m^{-2} d^{-1}. The lake lost 1.4×10^6 moles C in two weeks after ice melted by degassing CO_2, and 6.8 mmole C m^{-2} d^{-1} (1.5×10^6 moles) during the remainder of the open water period; 2.2 mmole C m^{-2} d^{-1} of this was release of CO_2 stored in the sediments by cryoconcentration the previous winter. Anaerobic microbial decomposition was only 4% of the benthic aerobic respiration rate of 38 mmole C m^{-2} d^{-1}. An annual budget estimate for the lake indicated that 50% of the carbon was produced by the benthic community, 20% by phytoplankton, and 30% was allochthonous material. The relative contribution of allochthonous input was in accordance with measurement of the $\delta^{15}N$ of sedimented organic matter.

Introduction

The Tuktoyaktuk Peninsula in the Northwest Territories of Canada is an abandoned delta formed during the Pleistocene era, that projects into the Beaufort Sea to the northwest of the modern Mackenzie River delta (Fig. 1). The numerous lakes of the peninsula are intensively used for feeding by juvenile broad whitefish *Coregonus nasus* (Pallas). The broad whitefish spawn in the Mackenzie River and larger numbers migrate as young of the year into lakes on the Peninsula and remain there for several years. Juvenile whitefish migrate into and out of the lakes during the open water period sometimes staying only the summer, sometimes as long as a few years. Upon reaching maturity, adult fish return to spawning sites, and reside in the Mackenzie Delta and Estuary (Bond & Erickson 1985; Chang-Kue & Jessop 1992; Lawrence et al.

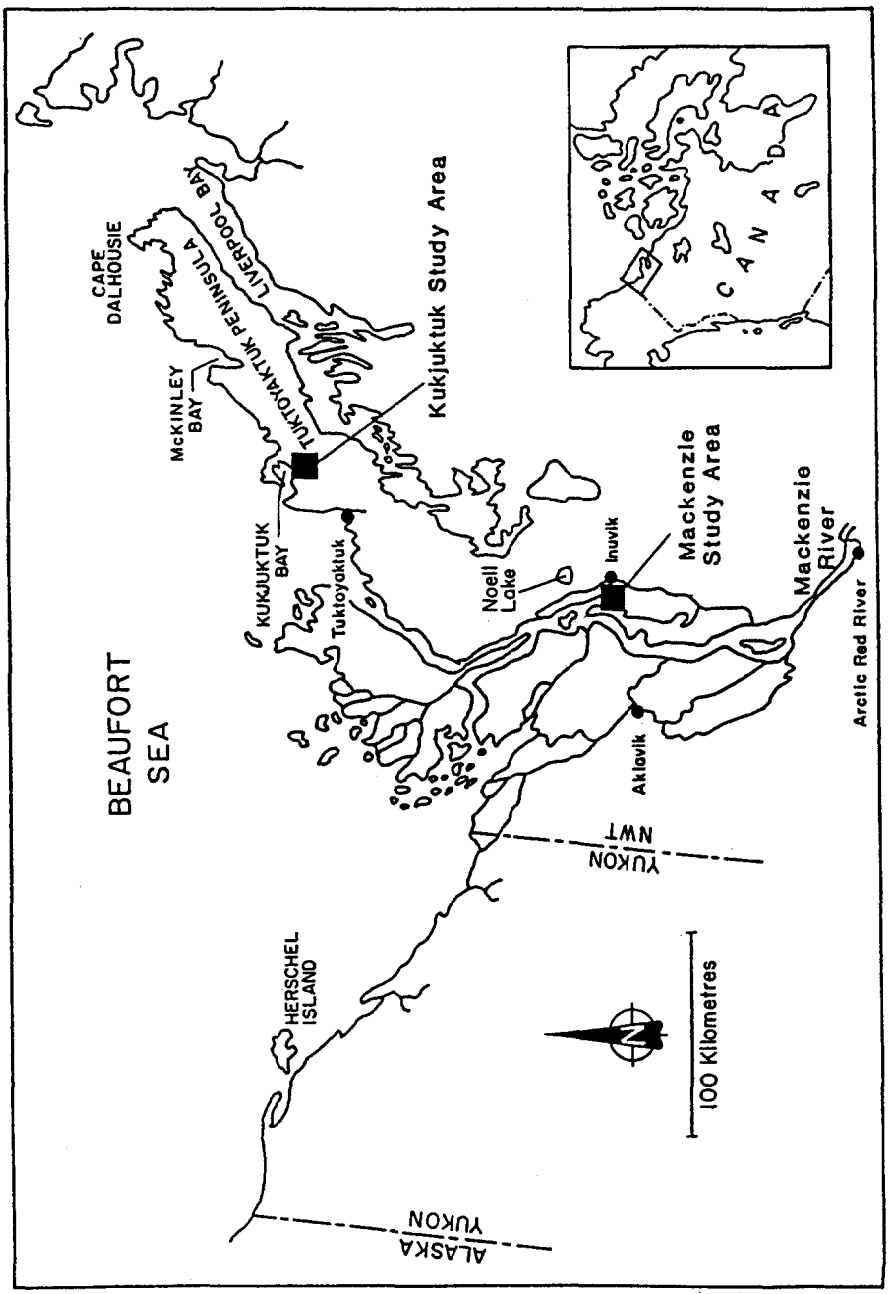

Fig. 1. Location of the Kukjuktuk lakes study area which contains Lake 18.

1984). The lakes on the Peninsula are critical feeding habitats for immature broad whitefish, and the organic carbon fluxes in the lakes may set potential limits on fish yields (Bodaly et al. 1989; Hesslein et al. 1991; Oglesby 1977).

We have defined the organic carbon budget for a Peninsula lake which we consider typical of the region. The approach taken was to estimate the overall annual carbon budget by measuring components important to the organic carbon budget during different seasons. The organic carbon budget can be expressed as:

$$O = P_p + P_B + P_I + R_P + R_B + S + \Delta P + P_O \quad (1)$$

where P_p = water column photosynthesis,
P_B = benthic photosynthesis,
P_I = allochthonous input of organic carbon,
R_P = water column respiration,
R_B = benthic respiration,
S = permanent burial in the sediments,
ΔP = change in organic carbon reservoir in the lake,
and P_O = loss of organic carbon at outflow.

We were not able to measure all of the components independently throughout the year, but during certain periods of the year components of the total carbon budget can be substituted to derive organic fluxes. The total carbon budget is defined as:

$$O = F_A + S + G_w + M_L + F_I - F_O + S_A \quad (2)$$

F_A = CO_2 flux through the air-water interface,
S = as above,
G_W = groundwater inputs,
M_L = change in mass in the lake,
F_I = input flux from surface water inflow,
F_O = flux in lake outflow,
and S_A = flux of CO_2 through the sediment-water interface.

We focused particularly on the contributions of the benthic plant communities (P_B and R_B) to equation (1) because a distinctive macrophyte community was visually abundant in these lakes, and such communities have been found to be important in other arctic lakes (Hobbie 1980; Kalff & Welch 1974). The metabolism of such communities have not been previously estimated in lakes of the western Canadian Arctic.

There are few organic carbon budgets for arctic lakes despite the importance of carbon fluxes in setting limits on secondary productivity, and the numerical importance of arctic lakes. Lakes and ponds of thermokarst origin or modified by thermokarst subsidence (Mackay 1963 in Sheath et al. 1975),

constitute 30–50% of the surface area of the Tuktoyaktuk peninsula. Most of these lakes are shallow (maximum depth approx. 4 m) and have nearshore areas composed of silts, clean sand, or cobble, and support prominent aquatic macrophyte communities (mainly of mosses and *Lemna*, Bond & Erickson 1985). Temperature, conductivity, and dissolved oxygen are homogeneous throughout the water column of these lakes during the ice-free season (Bond & Erickson 1982; Fee et al. 1988).

Previous studies of organic carbon budgets in the Arctic have been on small lake and pond systems in Alaska (e.g. Hobbie 1980; Whalen & Cornwell 1985) or in the eastern Canadian Arctic at Char Lake (Kalff & Welch 1974). The budget presented here is the first such budget from the western Canadian Arctic and allows inter-regional comparison of the productivity of these high latitude freshwater environments.

Materials and methods

Study area

Lake 18 is a typical Tuktoyaktuk Peninsula freshwater lake located in the Kukjuktuk stream basin at 69°30′30″ N, 132°28′00″ W (Fig. 1). The lake has an area of 282.8 ha, a maximum depth of 5.2 m and a mean depth of 1.45 m. The drainage basin area is approximately 61 km^2 with 81 lakes upstream of Lake 18. The lake is fed by a single major stream that enters from the south; its outflow exits to the north. The ice-free season is about 3 months for lakes in the vicinity of Tuktoyaktuk and 90 days has been used in our calculations. Maximum ice depth measured at the end of April was 1.3 m. Secchi depths as low as 0.7–0.8 m have been measured in the wave zone on windy days but values are generally 2.1–2.2 m at deeper sites (Fee et al. 1988). The lake is 22.5 km NE of the town of Tuktoyaktuk and is accessible only by air during the open water season. Like 18 is located in a region of continuous permafrost and was regularly monitored during the ice-free seasons in 1985 and 1986; laboratory analyses were done at the Inuvik Scientific Resource Centre, approximately one hour's flight from the lake.

Macrophyte collection and identification

Lake 18 supports an extensive macrophyte community consisting primarily of aquatic mosses and *Lemna trisulca*, between depths of 1–3 m (Ramlal et al. 1991). The extent and composition of these communities was established by laying out a transect from the shore to the maximum depth which was followed by SCUBA diver during July and August of 1985 and 1986. Quadrats of 0.05m^2 were sampled for macrophytes at each meter depth along this transect; only the above-sediment parts of the macrophytes were harvested. After the incubation of chambers in the lake, the material inside the chambers

was collected for identification and weight measurement. The mosses and *Lemna sp.* were not attached; therefore biomass in the sediment was likely very small on a whole lake basis. Samples were sorted by species, identified, and weighed (both wet and after drying to a constant weight at 60 °C). Carbon, nitrogen, and phosphorus concentrations in the plants were determined by combustion (Stainton et al. 1977) of a dried portion of each sample. Specimens were sent to the Canadian National Museum of Natural Sciences for identification. A reference collection is filed in the Department of Botany herbarium at the University of Manitoba.

Photosynthesis and respiration

Water column photosynthesis (P_p) was estimated using ^{14}C incubation and light intensity data with the numerical model of Fee (1984) (see Fee et al. (1988) for details). Oxygen concentration (O_2) changes in clear and dark acrylic (Plexiglas) chambers (0.5 m × 0.5 m × 0.15 m; designed by M. Holoka Freshwater Institute, Winnipeg) were used to estimate rates of benthic photosynthesis (P_B) and respiration (R_B). Attached to each of the chambers were battery operated magnetic stirrers, programmable timing devices used to select sampling intervals, and six glass syringes that contained preservative (NaOH solution made and added just prior to chamber installation; which increased the pH of sampled water to 11). The water overlying the sediment within the chambers was sampled by the syringes every 4 h. Paired chambers were set into the sediment at various depths by SCUBA diver five times between July 24 to August 19, 1986 and left for approximately 24 h. After the chambers had been placed in the sediment, duplicate 20 mL syringe samples for O_2 analysis were withdrawn through the serum stopper located at the top of each chamber (O_2 initial). Tritiated water (^3H_2O) was then added to each chamber; its concentration was used to determine chamber volume, and its distribution over time within the chambers enabled us to check that the contained water was thoroughly mixed and that no leakage occurred. At the end of the incubation period, two more 20 mL samples were taken from each chamber for O_2 oxygen analysis (O_2 final). Reagents to fix the oxygen were added to the syringes at the lake and the syringes were kept on ice during transport to the laboratory in Inuvik. The decrease of O_2 after 24 h in the dark estimates R_B (plant respiration and aerobic microbial decomposition). The O_2 change in the clear chambers estimates $P_B + R_B$. The difference between the rate of change in the two chambers thus estimates gross photosynthesis by benthic plants (P_B). Oxygen concentrations were measured with the Winkler method (Stainton et al. 1977) modified for small sample size, usually 15 mL. To be able to compare the results from the O_2 and CO_2 measurements, the results were converted to mmole CO_2 produced or consumed; 1 mmole O_2 consumed was assumed to be equivalent to 1 mmole CO_2 produced and vice versa, i.e., the respiratory and productivity quotients were assumed to be equal to one.

pCO_2 and gas exchange

The net flux of CO_2 (F_A) between the surface water and atmosphere was estimated for two periods during the open water season. During both periods the mass transfer coefficient (MTC) for CO_2 across the air-water interface was determined from wind speed using the relationship given by Wanninkhof et al. (1985) and Crusius & Wanninkhof (1990). For the first period immediately following ice melt (approx. July 5) during which we had no measurements of pCO_2 in the water or air, F_A was estimated as the loss of the excess CO_2 accumulated under the ice. The lake was assumed to mix vertically during this time uniformly distributing the CO_2. This was then degassed over a period of about two weeks as determined by the MTC. For the remainder of the open water period we based our estimate of F_A on measurements of pCO_2 in the surface water and in the air 2 m above the lake July 25–August 15, and extrapolated those results to the time of ice formation on October 1.

Atmospheric carbon dioxide ($pCO_{2(atm)}$) was sampled with a 50 mL glass syringe fitted with a 3.8 cm 22G needle; the syringe was held at arm's length over the lake surface, flushed several times, then approximately 7 mL was injected into an evacuated serum vial. Aqueous carbon dioxide ($pCO_{2(aq)}$) was sampled with a 0.5 L thermos bottle fitted with a two-hole rubber stopper. After filling the bottle gently, by displacement from the bottom, 25 mL of air was injected while displacing water from the bottom of the thermos. The thermos bottle was shaken vigorously for at least 2 minutes. The head space gas was sampled by withdrawing the gas while the apparatus was held underwater and allowing water to flow back into the bottom of the bottle, displacing the extracted equilibrated air sample. The gas was injected into an evacuated serum vial.

CO_2 was analyzed using a gas chromatograph equipped with a methanizer and a flame ionization detector (FID-GC) with a precision of 1% over the range of concentrations found. The difference between pCO_2 in surface water and air was used to calculate F_A, the flux of CO_2 through the air-water interface (positive values represent invasion of CO_2) from the lake in units of mole d^{-1} from the equation:

$$F_A = (pCO_{2(atm)} - pCO_{2(aq)}) \times MTC \times K \quad (3)$$

K = solubility constant of CO_2 (mole m^{-3} atm^{-1}),

at the *in situ* temperature.

Winter respiration

Whole-lake winter respiration $(R_P + R_B)_{winter}$ was estimated by measuring the change in the concentration of O_2 under the ice. The consumption of O_2 in the lake was calculated for the period of October 1, 1986 (the approximate freeze-up date) to April 28, 1987. Since we were unable to sample on

October 1, 1986, we assumed the water column temperature would be 1 °C and the O_2 would be at saturation (0.43 mM). Welch (1974) and Welch & Bergmann (1985) demonstrated that freeze-out of O_2 is close to 100%. Areal O_2 consumption was calculated by dividing the change in total mass of O_2 during the period (taking into account the volume of water at each depth interval) by the underice sediment surface area at the time of spring sampling. CO_2 production under the ice was assumed to be equal to the O_2 consumption. A portion of the CO_2 would have diffused into the pore waters over the winter period. A mean diffusion distance was calculated based on the effective diffusion coefficient in the Lake 18 sediments, and the mean depth of the under ice volume was increased by this amount to calculate the CO_2 in the water under ice just before spring melt. CO_2 in the water in the fall was assumed to have concentrated in the under ice volume by freeze-out as was the case for oxygen. This amount was added to that accumulated by respiration. The CO_2 concentration prior to freeze-up in the fall was estimated based on the summer measurements. The cryoconcentration factor was calculated to be 2.91 based on the increase in chloride concentration under ice. Cryoconcentration factors based on chloride give generally very good agreement with those calculated from ice thickness and bathymetry (Ramlal unpublished).

Stable isotope analysis

The stable isotopic compositions of nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) of dominant aquatic and terrestrial plant materials were analyzed to estimate the relative contributions of allochthonous and autochthonous organic materials. Dried samples were mixed with copper, copper oxide and a small piece of silver foil and placed in a 25 mm × 9 mm Vycor® tube and processed as per Hesslein et al. 1989. Carbon standards traceable to PDB ($\delta^{13}C$ = 0‰) and nitrogen extracted from air was used as the N standard ($\delta^{15}N$ = 0‰). Duplicate analyses typically had a standard deviation of 0.1‰ and 0.3‰ respectively.

Porewater chemical profiles

Profiles of dissolved methane (CH_4), sulfate, inorganic carbon (DIC), iron and manganese concentrations were measured in sediment porewater using two *in situ* multicelled porewater samplers similar to those described by Hesslein (1976), except that Nuclepore membrane (0.2 μm) was used instead of dialysis membrane. The profiles were used to calculate the diffusive flux rates of these chemical species from sediment to lake water, which were needed to estimate the rate of anaerobic carbon decomposition in the sediments. The samplers were inserted into the sediments at a lake water depth of 2.5 m and allowed to equilibrate with the dissolved chemical species in the porewater of the sediments for one week. As soon as the samplers were retrieved, water in selected cells was removed (total time 5–10 min). CO_2 and CH_4 sampling

was initiated just above the sediment – water interface and progressed downward. The samples were preserved by injecting them into evacuated serum vials containing 50 µL of 4% sulfuric acid (Kelly & Rudd 1984). In the laboratory, helium was injected into the vials until they reached atmospheric pressure. CO_2 and CH_4 were analyzed using the FID-GC with the methanizer.

Measurements of dissolved sulfate, iron and manganese were made on samples taken from a second sampler beginning at the deepest cell and progressing upward. The samples were put into small glass vials with Teflon® lined caps and analyzed using Dionex ion chromatography.

Sediment cores

Sediment cores (5 cm diameter) were collected using a K-B corer (Wildco Wildlife Supply Co.) in September, 1985 at a depth of 2.9 m. The cores were sliced in 1 cm sections and dried at 60 °C (drying at higher temperatures may drive off some volatile compounds). The porosity of the sediments was calculated as the volume of water evaporated per volume of sediment (Rudd et al. 1986). Carbon (± 4%), and nitrogen (± 5%) were analyzed according to Stainton et al. (1977). The sedimentation rate was calculated using results of ^{210}Pb analysis as described by Kipphut (1978). These analyses were done at the Freshwater Institute in Winnipeg.

Diffusion coefficients and flux rates

In situ diffusion coefficients and fluxes of CH_4, CO_2, bicarbonate, sulfate, iron and manganese out of the sediments were calculated from porewater concentration profiles and the sediment core data (with corrections for temperature changes). The porosity of sediments in Lake 18 (0.87–0.85) was similar to that of Woods Lake in the Adirondacks (0.95–0.77; Rudd et al. 1986), and we used the *in situ* diffusion coefficient for tritium determined in that paper (i.e., calculated from the penetration of tritiated water into Woods Lake sediments) to calculate the *in situ* diffusion coefficients of various substances in Lake 18 sediments based on water diffusion coefficients for dissolved substances (Li & Gregory 1974) and dissolved gasses (Himmelblau 1964).

Results

Macrophyte distribution and composition

The maximum depth of the lake was found in the small bay where our observations were made. The zone influenced by wave action, which normally extended to a depth of 1 m, contained little macrophyte material. The largest

biomass of plants and the most diverse community were found in the 1–2 m zone which encompassed more than 80% of the total lake area. This zone contained *Potamogeton* spp., *Lemna trisulca, Myriophyllum exalbescens* and a mixture of aquatic moss species, *Drepanocladus* sp., *Calliergon* sp. and *Fontinalis* sp. The rooted emergent and submerged species of *Potamogeton* and *Myriophyllum* were sparse (generally < 1 m^{-2}). Lemna could be found in the water column, but it was mostly lying on the bottom during the observation period. The sediment surface in the 1.5–2.5 m depth zone was continuously covered by an aquatic moss-*Lemna* community. This plant cover increased in thickness with depth apparently as wave energy became insufficient to redistribute material to greater depths. The aquatic mosses were not attached to the sediment and could be moved by wave action. The mosses, accumulating mainly between 1–3 m, contributed more than 90% to the total macrophyte biomass in the lake. During the SCUBA survey large piles of moss, some over 1 m in height, were noted. At depths > 2.7 m and down to approximately 4 m, the rhizobenthic charophyte *Tolypella intricata* was the only macrophyte present. No macrophytes were observed at depths > 4 m; microscopic algae may have been present in the apparently bare, fine-grained sediment. Similarly microscopic algae were present on the bare sediments < 1 m in depth.

A number of macrophytes were collected from Lake 18 by SCUBA divers during 1985 for chemical analysis. The carbon, nitrogen and phosphorus content differed between those plants attached to the sediments, *Potamogeton*, *Myriophyllum* and *Tolypella* and those non-attached macrophytes lying on the sediments. The rooted groups had higher P content and lower C:N:P molar ratios; within taxa there was no evidence that nutrient composition was depth dependent. Elemental nutrient ratios (C:N:P; 305:16.4:1) were generally indicative of nutrient sufficiency in macrophytes (Atkinson & Smith 1983).

Phytoplankton photosynthesis

The ^{14}C method as used here to estimate phytoplankton photosynthesis has been found to approximate gross photosynthesis (Bower et al. 1987). Volume weighted daily means were corrected for the decrease of lake volume with depth (Table 1; Fee 1980). A mean of 6.3 mmole C m^{-2} d^{-1} was calculated from the five daily estimates for the days on which benthic photosynthesis and respiration were measured. The integrated value for the open water period of 90 days was 0.43 mole C m^{-2} y^{-1} calculated from daily irradiance and tri-weekly measurements of photosynthetic parameters.

Benthic photosynthesis and sediment respiration

In all cases, more O_2 was produced in the clear chambers than in the dark chambers; nevertheless, the overall concentration of O_2 decreased in the clear chambers during the incubation period, indicating community respiration

Table 1. Whole lake volume integrated water column photosynthesis ^{14}C method, data from Fee et al. (1988) for Lake 18, 1986.

Date	mmole m^{-2} d^{-1}
Jul 25	7.23
Jul 29	5.09
Aug 8	7.24
Aug 14	7.53
Aug 18	4.15
Mean	6.25
Standard deviation	1.25

Time integrated value from Fee data using actual irradiance for the 90 day open water period = 0.43 mole m^{-2} y^{-1}.

consistently exceeded photosynthesis (Fig. 2). Oxygen consumption (dark chambers) as carbon equivalents was similar at all depths, ranging from 32–47 mmole C m^{-2} d^{-1} (Table 2). Benthic photosynthesis was highest within the 1.3–2.0 m contours and lowest at 2.5 m. Photosynthesis in the 0–1.3 m depth interval was extremely high relative to the macrophyte biomass (Table 2); this probably reflects the high metabolic rates of benthic algae, as only these photosynthesizing organisms are present in the wave influenced zone. The 1.3–2.0 m depth interval was the most important site of photosynthesis in the lake because it includes more than 80% of the sediment surface and gross photosynthesis was highest in that interval although net was still negative. Of the total biomass of macrophytes incubated within the chambers, 40–80% consisted of brown, not photosynthetically active, material.

The areal weighted mean for gross benthic photosynthesis (Table 2), was 31.2 mmole C m^{-2} d^{-1}, nearly 5× the phytoplankton rate of 6.3 mmole C m^{-2} d^{-1}. Gross benthic respiration was 38 mmole C m^{-2} d^{-1}. The areal weighted net benthic flux added 6.6 mmole C m^{-2} d^{-1} to the water column as CO_2. We used a value of respiration at 2.5 m (32.4 mmole C m^{-2} d^{-1}) as our estimate of R_B for depths > 3 m and assumed no photosynthesis occurred because it was likely that photosynthesis at these depths was extremely low due to light limitation. Because less than 5% of the lake's area was > 3 m depth, assumptions made about photosynthesis and respiration at these depths do not seriously affect whole lake totals. Depths to which 1% of surface light penetrated ranged from 3.3–5.7 m throughout the period of our experiments in 1986.

Winter respiration

Both winter O_2 consumption and CO_2 production (Table 3) were calculated on the basis of the underice sediment surface area when the ice thickness was 1.3 m, which is equivalent to 1.17 m of water. O_2 consumption was estimated as 0.87 mole O_2 m^{-2} under the ice.

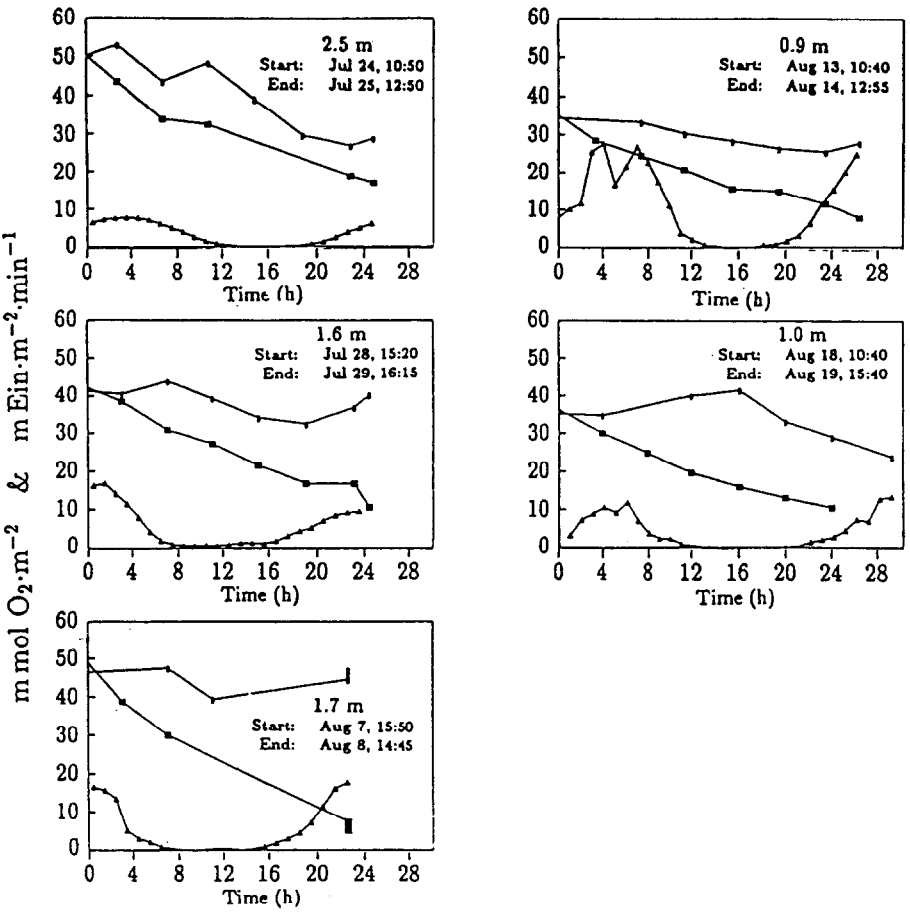

Fig. 2. Oxygen measurements in the clear (+) and dark (■) chambers, and irradiance (▲) in the clear chambers. Irradiances have been corrected for attenuation at depth.

We estimated the CO_2 accumulation to be equal to the O_2 consumption plus the cryoconcentration (2.91) of the ~60 μmole CO_2 L^{-1} in the water in the fall, or 0.87 + 0.13 = 1.00 mole m^{-2}. The mean diffusion distance into the sediments was about 0.16 m ($x = \sqrt{(2\,D\,t)}$, D = 0.6 cm^2 d^{-1}, t = 210 d). This increases the effective sub-ice volume for CO_2 by 32%. The expected CO_2 in the water would then be 0.76 mole m^{-2} or an average of 1.00 mole m^{-3} in the sub-ice volume. A single measurement of CO_2 at 2 m under the ice surface was 0.75 mole m^{-3} (DIC = 3.44 mole m^{-3}). A gradient of CO_2 likely existed in the sub-ice water so we consider the measurement to be consistent with the calculated value. This winter respiration rate (4.1 mmole m^{-2} d^{-1}) was approximately 10% of the daily summer benthic respiration rate. We calculate that 1.86 × 10^6 mole CO_2 would have accumulated over the 9 months of ice cover (1.6 × 10^6 moles from respiration and 0.26 × 10^6 moles from

Table 2. The carbon budget of the benthic communities during the ice free season (1986) of Lake 18. R_B = respiration, P_B = photosynthesis (gross calculated by difference), mean = mean for depth interval.

Contour interval m	Sediment area ha	Volume m^3	Incubation depth m	Macrophyte green biomass $g \cdot m^{-2}$	Macrophyte brown biomass $g \cdot m^{-2}$	R_B meas. mmole m^{-2} d^{-1}	R_B mean mmole m^{-2} d^{-1}	$R_B - P_B$ calc. mmole m^{-2} d^{-1}	$R_B - P_B$ mean mmole m^{-2} d^{-1}	P_B calc. mmole m^{-2} d^{-1}	P_B mean mmole m^{-2} d^{-1}
0–1.3	98.5	3056583	0.9	0.3	1.5	34.0		8.0		26.0	
			1.0	88.5	262.4	34.0	34.0	8.8	8.4	25.2	25.6
1.3–2.0	150.5	712324	1.6	12.4	87.3	36.1		1.4		34.7	
			1.7	151.6	102.8	46.7	41.4	0.9	1.2	45.8	40.3
2–3	19.9	227115	2.5	na	na	32.4	32.4	21.0	21.0	11.4	11.4
3–5.2	13.5	112145				32.4	32.4	32.4	32.4	0.0	0.0
Area weighted mean						37.8		6.6		31.2	

Table 3. Late fall (1986) and spring (1987) O_2, Cl, and CO_2 and ancillary measurements required to calculate winter respiration. Fall DIC and Cl estimates were extrapolated from September 4 measurements. O_2 was assumed to be at saturation at 1 °C.

Quantity	Fall 1986	April 28, 1987
Mass of O_2 in Lake 18 (mole)	1.75×10^6	0.14×10^6
Cl (mmole L^{-1})	0.310	0.903
Cl cryoconcentration factor	na	2.91
$CO_{2(aq)}$ measured (mmole L^{-1})	0.060	0.745
DIC measured (mmole L^{-1})	1.24	3.44
Ice thickness (m)	na	1.3
Subice sediment surface area (ha)	na	185.6
Water temperature (°C)	1.0	0.0–2.3

na: not applicable

cryoconcentration), 0.46×10^6 moles (32%) in the sediments and 1.4×10^6 in the water column.

Porewater profiles and sediment chemistry

In the sediment porewater profile of dissolved chemicals (Fig. 3), the most apparent feature was the high concentration of DIC in the sediments compared to the overlying water. Sulfate penetrated to a depth of 3 cm in the sediment, whereas CH_4 and dissolved manganese concentrations were constant at depths > 5 cm and dissolved iron increased at greater depths. Based on the *in situ* diffusion coefficient (see Methods) and the maximum concentration gradients, the flux of each chemical species was calculated (Table 4).

By converting the rate of reduction of electron acceptors to CO_2 equivalents according to the Redfield ratio of organic carbon consumption (from Froelich et al. 1979 in Kelly et al. 1982), anoxic decomposition was determined as described by Kelly et al. (1982). Because methanogenesis produces approximately one molecule of CO_2 for every molecule of CH_4, the flux rate for CH_4 was doubled to estimate C production from anaerobic metabolism. Therefore in C equivalents, methanogenesis produced 1.41 mmole m^{-2} d^{-1}; and when included with sulfate, iron, and manganese reduction (in CO_2 equivalents) the total was 1.62 mmole m^{-2} d^{-1}. Thus, methanogenesis accounted for more than 85% of the total measured anoxic decomposition.

If we assume CO_2 flux from methanogenesis to be 0.7 mmole m^{-2} d^{-1}, as above, the remaining DIC flux is 6.6 mmole m^{-2} d^{-1} (Table 4). This flux is the result of the stored DIC in sediments from under-ice accumulation. Based on the fraction of CO_2 in DIC under the ice (0.75/3.44 = 0.22, see Winter Respiration) we estimate the total CO_2 flux by diffusion from the sediments to be $0.22 \times 6.6 = 1.5 + 0.7$ (methanogenesis) = 2.2 mmole m^{-2} d^{-1}

The sedimentation rate for the core location calculated from ^{210}Pb profiles in the sediment was 90 g m^{-2} y^{-1} and the buried carbon content of the sediment

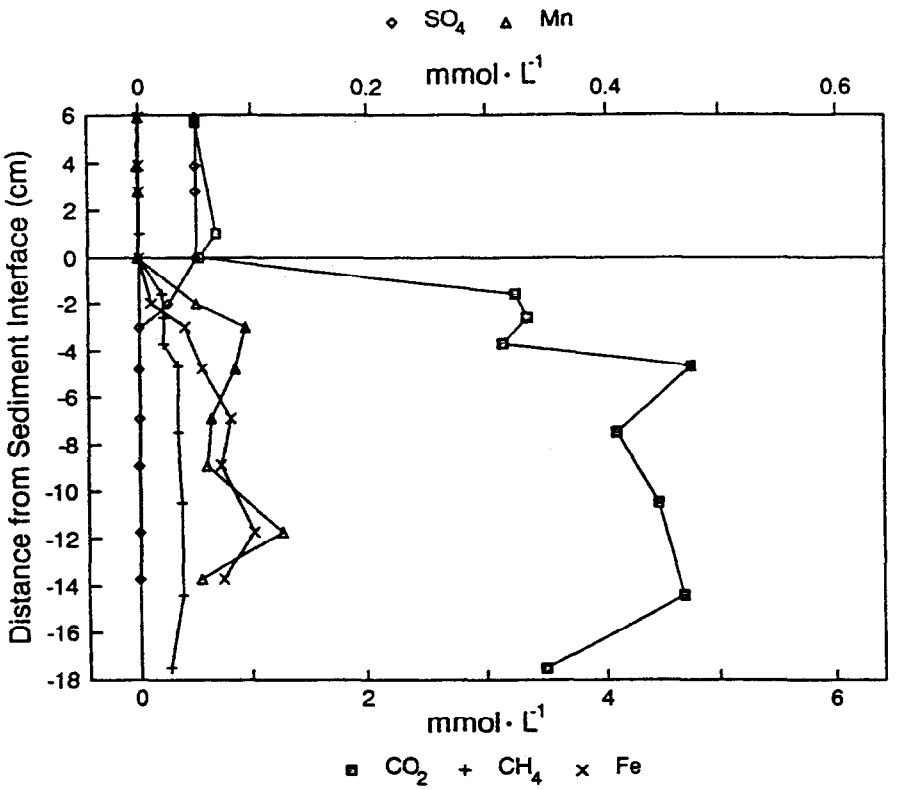

Fig. 3. Porewater chemistry profiles from Lake 18 sediments. Samplers were in place 24–31 July, 1986.

Table 4. Maximum concentration gradients, functional diffusion coefficients, and fluxes from the sediments to the water for dissolved components in Lake 18 sediments. Negative values indicate flux from water to sediments. Concentration gradients are from close interval porewater sampler set at 2.5 m in July 1986.

Component	Gradient mmole cm^{-4}	Diffusion coeff. $cm^2\ s^{-1}$	Flux mmole $m^{-2}\ d^{-1}$
CH_4	0.124×10^{-3}	6.63×10^{-6}	-7.7×10^{-1}
DIC[a]	1.696×10^{-3}	5.00×10^{-6}	-7.3
SO_4	-0.017×10^{-3}	3.81×10^{-6}	5.5×10^{-2}
Fe	0.123×10^{-3}	2.55×10^{-6}	-2.7×10^{-1}
Mn	0.030×10^{-3}	2.41×10^{-6}	-6.3×10^{-2}

[a] Diffusion coefficient estimated from CO_2 and HCO_3^-

was 3.41 mmole g^{-1}; the buried nitrogen content of the sediment was 0.28 mmole g^{-1}. Therefore, 0.31 mole C m^{-2} y^{-1} was deposited in the sediment on a long term basis at the core site.

Air-water CO_2 flux

The mass transfer coefficient (MTC) for transfer across the air-water interface was estimated from the mean wind speed measured at Tuktoyaktuk of 2.2 m^2 s^{-1} (B. Fallis, Freshwater Institute, unpublished data) and the relationship between MTC and wind speed for SF_6 in small lakes (Crusius & Wanninkhof 1990; Wanninkhof et al. 1985). Correcting for the differences in molecular diffusivities between SF_6 and CO_2 (0.73×10^{-5} cm^2 sec^{-1}, 1.2×10^{-5} cm^2 sec^{-1} respectively, and $MTC_2 = MTC_1 \times \sqrt{(D_2/D_1)}$ we calculated MTC = 0.31 m d^{-1}. Based on the data of Wanninkhof et al. (1985) and Crusius & Wanninkhof (1990) the uncertainty is about 20%. Since the mean depth of the lake is 1.45 m the mean response time for gas exchange is about 4.7 days or a half-time of about 3.2 days. The melting of the ice and mixing of the lake would have resulted in CO_2 = 0.375 mole m^{-3} or 6000 µatm (at 6 °C). This would have decreased to 400 µatm in 13 days. After this initial period of degassing of winter CO_2, we estimated F_A from the measured difference in pCO_2 between the water and the air (Table 5). The mean excess of pCO_2 in the lake was 408 µatm or 0.022 mole m^{-3}. The calculated flux is 6.8×10^{-3} mole m^{-2} d^{-1} from the lake to the atmosphere.

Table 5. Lake 18 air and surface water pCO_2 data for 1986. pCO_2 units are µatm.

Date	Lake temp. °C	pCO_2		
		Air	Water	ΔpCO_2
Jul 25	10.9	402	915	−513
Jul 29	10.6	367	460	−93
Jul 30	10.6	522	1083	−561
Aug 8	12.0	500	747	−247
Aug 13	13.1	495	1099	−604
Aug 19	10.4	700	1128	−428
Mean	11.3			−408 ± 182

Water column respiration

Water column respiration was calculated by solving

$$O = F_A + S_A + (P_P + P_B + R_P + R_B) + M_L \quad (4)$$

for the unknown quantity R_P (Table 6). The solution gives a value of 4.4 ± 3.6 mmole C m^{-2} d^{-1}, slightly less than the measured rate of plankton

Table 6. The respiration in the water column of Lake 18 by difference of other water column processes (mmole m^{-2} d^{-1}).

F_B	−6.8 ± 1.7
S_A	2.1 ± 0.07
$R_B - P_B$	6.6 ± 2.2
P_P	−6.3 ± 2.2
M_L	0.0 ± 0.3
R_P (sum)	−4.4 ± 3.6

photosynthesis of 6.3 mmole C m^{-2} d^{-1}. The difference between measured phytoplankton photosynthesis and estimated water column respiration (net carbon fixation) falls within the error of either method, suggesting that sedimentation of phytoplankton primary production is not a significant input to benthic respiration. Bower et al. (1987) in the course of a whole lake radiocarbon experiment observed sedimentary losses of photosynthetically fixed carbon from the epilimnion to be on the order of 1–17% of photosynthesis and within the error of their estimate of photosynthesis. The lake studied by Bower et al. (1987) was a 16 ha temperate, stratified lake with a 3 m mixed layer. Although our estimate of water column respiration is derived by difference, it is consistent with the data of Bower et al. (1987) which is the most direct and quantitative treatment of the fate of carbon fixed by phytoplankton to date.

Stable isotope analysis

Biota collected from Lake 18 (Fig. 4) had $\delta^{15}N$ values between 5.0 and 8.2‰. The $\delta^{15}N$ values from the sediment were lower and ranged from 2.3 to 4.7‰. *Salix* sp. from near South Lake on the Mackenzie Delta (68°18′ N; 133°51′ W) were the only terrestrial material available for comparison. This genus is prominent in tundra vegetation of the Tuktoyaktuk Peninsula and indicate possible nitrogen ratios for terrestrial vegetation. The $\delta^{15}N$ values from *Salix* (−1.5 to 1.3 ‰) were similar to those found in terrestrial material collected from the Experimental Lakes Area in northwestern Ontario (R. H. Hesslein, unpublished data) and may represent a reasonable substitute for Tuktoyaktuk vegetation. The sediment $\delta^{15}N$ values suggest a mixture of two sources; the more enriched ^{15}N in plankton and mosses and the ^{15}N poor terrestrial vegetation. Apart the *Lemna* sp. ($\delta^{13}C$ = −16.5 to −18.5‰) the $\delta^{13}C$ signal was similar in all materials measured ($\delta^{13}C$ = −24.5 to −28.7‰).

Discussion

The annual carbon budget of Lake 18 can best be tabulated for three physicochemical seasons: 1. The winter period when the lake is ice covered from

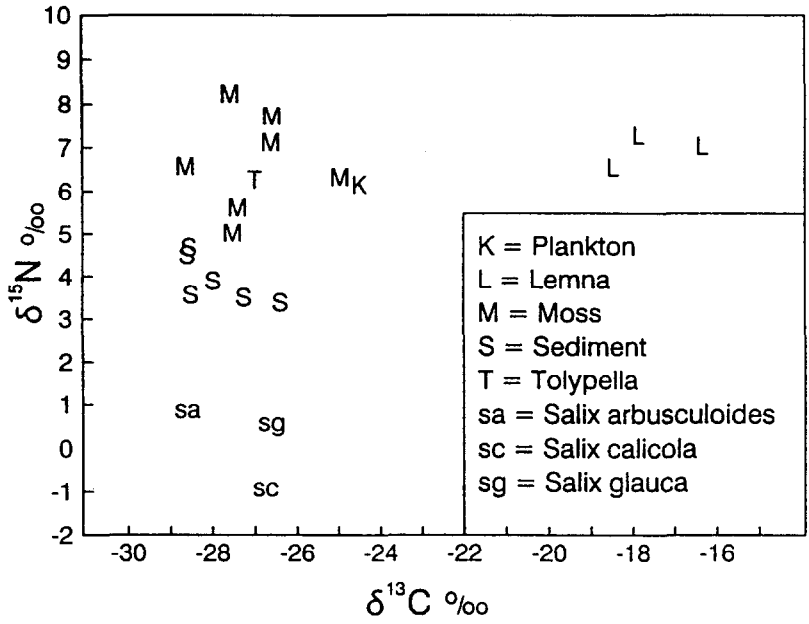

Fig. 4. Stable isotope results of biota and sediments from Lake 18 and terrestrial material from the Mackenzie Delta.

early October to early July; 2. A two week period just after the snow and ice have melted when flows are high and CO_2 built up under the ice is degassed; and 3. The subsequent open water period of 77 days when flows are low and controls on carbon concentrations in the lake are dominated by internal processes.

One difficulty in establishing a mass balance for carbon in Lake 18 is the uncertainty of the water budget. There have been no rigorous studies of precipitation and runoff on the Tuktoyaktuk Peninsula. There is a 30 year record of precipitation at Tuktoyaktuk with mean annual value of 126 mm. This is one of the lowest in Canada. An estimate of runoff was made by Chang-Kue et al. (1992) in 1979 by daily velocity measurements in a cross-section of Kukjuktuk Creek just above the zone of tidal influence. In 1979 low flow over the ice in Kukjuktuk Creek began near the beginning of June and increase very rapidly around the 12th of June. Flow stayed high until July 7th and then decreased by 70% to the end of July at which level it remained until freezing near Oct 1. The integrated annual outflow was 2.4×10^6 m^3 which yields only 8 mm of runoff when divided by our estimate of the area of the Kukjuktuk Creek watershed; 280 km^2. This amount of runoff would result in a water residence time of 8 years for Lake 18. In 1990 a gauging station was established on Freshwater Creek which drains a very similar sized watershed (approximately 280 km^2) to that of Kukjuktuk Creek and is directly adjacent to it. Our calculations using the preliminary flow

results (Moe Hansen, IWD, Dept. of Environment, Inuvik, N.W.T., personal communication) yield an annual runoff of 28 mm. This gives a water residence time of 2.3 years for Lake 18. From these limited data we can only conclude that the water residence time is 2–8 years, which unfortunately covers the range over which flushing goes from important (43% per year) to unimportant (13% per year) with respect to calculating the carbon budget for the open water period. We believe that we can work around this uncertainty.

The winter condition is relatively straightforward as described in the Results section. Oxygen is consumed and CO_2 produced by the respiration of organic matter on and in the sediments. Cryoconcentration proceeds as the ice layer is formed. The combination of these two processes and the long ice covered period result in an estimated 32% of the CO_2 diffusing into or remaining in the sediments. The uptake of oxygen was estimated to be 2.1×10^6 moles, with an equivalent amount of CO_2 produced, and 1.4×10^6 moles of that CO_2 accumulating in the water column. In terms of the total carbon budget of the lake, no net input or output processes are active during the winter period. That is, the lake was not receiving any new carbon, or releasing any of the processed carbon.

The two week length of the degassing period after iceout is defined by the MTC for gas exchange of 0.31 m d^{-1} (see Results). Based on this rate and the mean depth of 1.45 m, two weeks is the time needed for 95% of the excess CO_2 present in the lake when the ice disappears, to be lost to the atmosphere. Using the two available stream hydrographs, about 20% of the annual flow can occur during these two weeks. This would flush only 2–9% of the lake volume. Because most of the inflowing water comes from upstream likes, the CO_2 concentrations in the inflow are not likely to be much different than in Lake 18, and are certainly unlikely to be much higher. Based on the above arguments we neglect the effect of surface water flow on the CO_2 flux during the two week period of degassing.

Mean open water rates of gross phytoplankton CO_2 uptake (Table 1) were only one tenth the average degassing rate estimated for the two week period. The benthic chambers (Table 2) showed a flux of CO_2 to the lake of similar magnitude to the gross production. We feel it is very unlikely that photosynthesis could have significantly contributed to the loss of CO_2 during the two week period. Our estimate for the two week period is that the net CO_2 flux is best represented by the loss of all of the 1.4×10^6 moles accumulated under the ice.

The summer period is characterised by very low flow due to higher evaporation and low precipitation. Based on the hydrologic records, the summer flows could result in a gross exchange of lake water of only 0.08–0.3% d^{-1}. This rate is equivalent to an MTC of only 0.0016–0.0044 m d^{-1}, only about 1% of the MTC for that we determined gas exchange (see Results). For the water flows to supply a significant portion of the estimated loss of CO_2 due to gas exchange the CO_2 concentrations in the inflowing water would have to have been 100 times that in the lake. This is impossible for

the surface inflow, most of which comes from the lakes and streams in the large drainage basin of Lake 18. Concentrations as high as that are unlikely but not impossible for ground waters. Ground water flows have not been measured in this area but they are unlikely to be important inputs of CO_2 to the lake. Lake 18 is at the outflowing end of a drainage basin 23 times its surface area and half covered with lakes. Most of the snowmelt runs off from frozen ground. In this setting, it is hard to imagine that groundwater represents a significant fraction of the total flow. If the fraction of total flow was small, the CO_2 in groundwater would have to be hundreds to thousands of times the excess CO_2 in the lake to account for the observed loss of CO_2 in the lake. This is far above any observations of groundwater CO_2 in northern latitudes. Furthermore, the fluxes calculated from porewater profiles and measured in the sediment flux boxes would have included groundwater contributions in those locations in Lake 18.

On the basis of the above arguments we have ignored fluxes of CO_2 resulting from water flow during the summer period. Therefore we were able to define the summer CO_2 mass balance in equation 3;

$$O = F_A + S_A + (P_P + P_B + R_P + R_B) + M_L$$

that is, barring addition of acid or base which would alter the relationship between DIC and CO_2, the CO_2 is controlled by its flux at the boundaries; air and sediment, the internal conversions between the CO_2 pool and the organic pool (respiration and production), and the change in mass. The mass of CO_2 is variable, as represented in the data in Table 5, but no long term change is apparent. A change of 500 μatm in CO_2 (0.027 mole m^{-3} or 0.039 mole m^{-2}), the maximum that could be postulated from Table 5, results in $M_L = 5.1 \times 10^{-3}$ mole m^{-2} d^{-1}. This can be considered as a maximum estimate of uncertainty for M_L. We have adopted a mean of 0 with a standard deviation of 0.3×10^{-3} mole m^{-2} d^{-1} for M_L. We estimated total flux of CO_2 due to pore water diffusion to be 2.2×10^{-3} mole m^{-2} d^{-1}. This included the return of CO_2 which diffused into the sediments in winter (1.5×10^{-3} mole m^{-2} d^{-1}) as well as CO_2 produced by methanogenesis (0.7×10^{-3} mole m^{-2} d^{-1}). If we distribute the estimated amount of CO_2 stored in the sediments during winter, 0.46×10^6 moles (see Results) as a uniform flux over the summer period, the flux estimate is 1.8×10^{-3} mole m^{-2} d^{-1}, in very good agreement with the flux estimated from pore water concentrations.

Before using equation (4) to calculate R_P, let us consider exactly what fluxes were measured by the oxygen changes in the flux boxes. Oxygen could be consumed by two processes, 1. respiration by benthic biota; and 2. oxidation of methane diffusing from the sediment. The oxygen use by oxidation of the methane flux (0.7×10^{-3} mole m^{-2} d^{-1}) was measured as part of $(P_B + R_B)$ in the boxes and the CO_2 was estimated to be produced at an equal rate. A schematic of the fluxes into the light and dark boxes is shown in Fig. 5.

With the above clarifications of the summer fluxes an estimate of R_P can

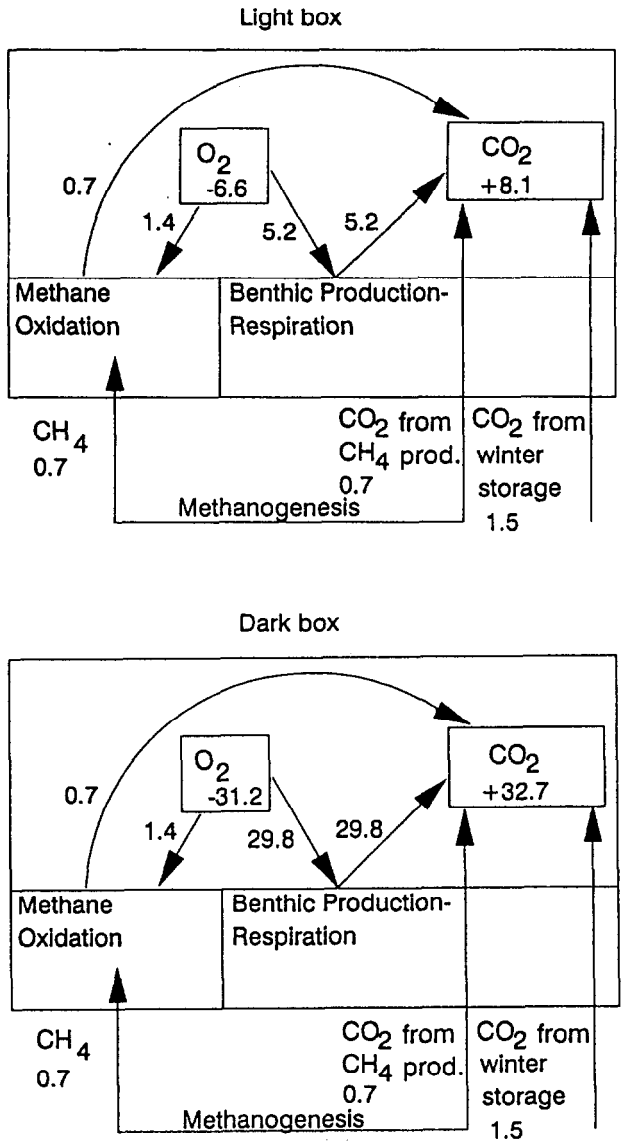

Fig. 5. Schematics of average fluxes as they would have existed in the clear and opaque boxes placed over the benthic communities. Units are in mole C m^{-2} y^{-1}.

be made using equation (4). This appears in Table 6. Water column respiration is estimated to be $4.4 \pm 3.6 \times 10^{-3}$ mole m^{-2} d^{-1}. When compared to the ^{14}C estimate of gross CO_2 uptake ($6.3 \pm 2.2 \times 10^{-3}$ mole m^{-2} d^{-1}) net water column production is $2.0 \pm 2.9 \times 10^{-3}$ mole m^{-2} d^{-1}.

Based on the above seasonal assessments of the CO_2 budgets it is possible to define the annual budget for CO_2 as in Equation 2:

$F_A = O_{\text{winter}} - 1.4 \times 10^6{}_{\text{spring}} - 1.5 \times 10^6{}_{\text{summer}} = -2.9 \times 10^6$ moles
G_w = ignored
$M_L = O_{\text{annual}}$
$F_1 - F_0 = O_{\text{annual}}$
$S_A = -0.5 \times 10^6{}_{\text{winter}} + 0.6 \times 10^6{}_{\text{spring+summer}} = 0.1 \times 10^6$ moles
$P_P + R_P = O_{\text{winter}} - 0.5 \times 10^6{}_{\text{spring+summer}} = -0.5 \times 10^6$ moles
$P_B + R_B = 1.6 \times 10^6{}_{\text{winter}} + 1.7 \times 10^6{}_{\text{spring+summer}} = 3.3 \times 10^6$ moles

The budget is in balance. The internal lake processes which are involved in the conversion of CO_2 to organic matter and vice versa ($S_A + P_P + R_P + P_B + R_B$) result in a net production of CO_2 (destruction of organic matter) of 2.9×10^6 mole y^{-1}. This is lost through the air-water interface. An external source of organic matter is required to support these fluxes. In addition, 0.9×10^6 moles of carbon are buried annually in the sediments which must also be supplied (total = 3.8×10^6 mole y^{-1}). Differences in particulate (POC) or dissolved carbon (DOC) in inflow-outflow or detrital transport from the local drainage are possible sources.

Given the water residence of 2–8 y, a difference in DOC + POC between inflow and outflow of 1.9 to 7.4 mmole L^{-1} would be necessary to supply the organic material. The concentration of DOC in Lake 18 is only ~0.4 mmole L^{-1} (Anema et al. 1990a,b), and although the inflow concentrations are not known, because the inflow comes mostly from the outflow of upstream lakes it is unlikely to contain enough DOC. POC concentration in the lake in the summer is only ~0.05 mmole L^{-1} (Anema et al. 1990a,b). We therefore conclude that the extra carbon is supplied as terrestrial detritus. This conclusion is supported by the $\delta^{15}N$ analyses of nitrogen stored in the sediments (Fig. 4). If the source of the sediment nitrogen was autochthonous the expected $\delta^{15}N$ values would be the same as the biota (Peters et al. 1978) or heavier (Pang & Nriagu 1977). If the sediment material had a significant amount of terrestrial material then a lighter signal would be expected (Peterson & Fry 1987). Because the sediment nitrogen signal is approximately half way between that of terrestrial and lake generated material at least 50% of the sediment nitrogen as a multi-year average must be allochthonous. If allochthonous sources made up all of the 3.8×10^6 moles missing in the carbon mass balance at least 12% would have been buried. Of the total gross autochthonous production ($(P_B + P_P) = 9.6 \times 10^6$ moles) something less than 5% would have been buried in the sediments. These estimates depend on the C:N ratio in the allochthonous and autochthonous being the same. The actual C:N ratio of the allochthonous input is unknown. It is likely to be higher than the mean C:N ratio of autochthonous production because of the higher cellulose content of terrestrial biomass (although in Lake 18 the abundance of macrophytes might reduce the difference) and because decomposition would have begun in the terrestrial regime (Wetzel 1975). Therefore, the allochthonous input may be expected to be more resistant to decomposition within the lake, and consequently the terrestrial input would be more prominent in buried sediments.

In any case, the stable isotope composition of the sediment material indicates that our estimate of the allochthonous carbon input is of the right order of magnitude. The possibility of compensating errors in the budget cannot be ignored since when solving by difference, all errors accumulate in this term. However, there are enough independent checks in our budget to suggest that no major term is grossly in error. Allochthonous inputs probably amount to 50% of in-lake photosynthesis and are apparently more important then phytoplankton photosynthesis in the carbon metabolism of this lake. Benthic photosynthesis is the most important organic carbon source for the lake and may account for 50% of all fixed carbon "available" to lacustrine food chains. Heavy ice and snow cover is likely to preclude significant photosynthesis prior to ice-out although we have no direct measurements. Hobbie (1964) reports that a large proportion of annual phytoplankton production (up to 80%) can occur in deep lakes underice if it is clear of snow. However, Welch et al. (1989) found that the proportion of underice production to annual phytoplankton production was strongly depth dependent in arctic lakes. In their shallowest lake, mean depth 1.8 m, under ice production accounted for less than 10% of annual production because a high proportion of the lake volume (77%) was frozen in the spring. Ice volume occupies a similarly high volume in the spring in Lake 18. We have not applied a 10% correction to our estimate of plankton primary production because it lies within the error of the open water measurement (15–20%). Welch & Bergmann (1985) also dismiss benthic primary production during the ice-covered period. Consequently we have extended our measured rates of photosynthesis and respiration throughout the open water period of early July through September and assume no significant photosynthesis prior to ice out. By doing this and estimating winter respiration, we can produce annual estimates of in-lake processes and solve for the net watershed contribution by difference.

Often, when primary production is considered in freshwater systems the emphasis is on phytoplankton photosynthesis (e.g. Sheath et al. 1975). This may be valid in deep, steep-sided lakes, but in shallow lakes, especially those with high transparencies (or lakes with large littoral zones), the site of maximum photosynthesis may be benthic. In our study, as in some others (e.g. Hargrave 1969; Welch & Kalff 1974), benthic photosynthesis by far dominated the in-lake photosynthesis (Table 7). Welch & Kalff (1974) summarized four studies which included measurements of benthic photosynthesis that showed that in large shallow lakes, or deep lakes with a "thick chlorophyll layer (moss, macrophytes, etc.)", more than 75% of the lake production was benthic; this characterization fits Lake 18 well.

In Lake 18 there was no relationship between green macrophyte biomass and benthic respiration. The epipelic algal-community at our shallowest site had rates of photosynthesis and respiration similar to deeper sites with high macrophyte biomass (Table 2). There are two possible explanations for this. One is that the benthic algal community is the predominant contributor to photosynthesis at all depths. Alternatively, the moss-Lemna community may

Table 7. Comparison of annual photosynthesis and respiration in Arctic and temperate lakes.

	Alaskan ponds (Arctic)	Char (Arctic)	Toolik (Arctic)	Lake 18 (Arctic)	Lawrence (Temperate)
Mean depth (m)		10.2	7.0	1.45	5.89
Maximum depth (m)	0.5	27.5	25	5.2	12.6
Open water temp. (°C)	max 6.1–8.4	max < 4.0	surface 16 bottom 7	mean 9.2	min 4 max 26
Open water season	70–90 d	0–42 d	90 d	90 d	April–Nov
	Photosynthesis (mole C m^{-2} y^{-1})				
Phytoplankton	0.09	0.34	1.17	0.43[1]	3.61
Benthic algae	0.70	1.48[1,2]		2.81[2]	3.32[3]
Marcrophyte	1.37				7.32
Total	2.16	1.82	1.17	3.24	14.25
	Respiration and decomposition (mole C m^{-2} y^{-1})				
Aerobic[4]	4.2[5]	1.36	0.56	4.27[6]	9.78
Anaerobic (benthic)			0.15		
Reference	a	b, c, d	e, f		g

a Hobbie (1980)
b Welch & Kalff (1974)
c Kalff & Welch (1974)
d Schindler et al. (1974)
e Whalen & Cornwell (1985)
f Miller et al. (1986)
g Wetzel et al. (1972)
[1] gross photosynthesis
[2] benthic algae + macrophyte photosynthesis
[3] epiphyte and epipelic algae photosynthesis
[4] including winter and phytoplankton respiration where available
[5] estimated from CO_2 gas evasion measurements similar to those used in this paper
[6] integral phytoplankton photosynthesis × R_P/P_P from Table 6 used for integral R_P

shade the epipelon community at greater depths. The dominant macrophyte community (Lemna and aquatic moss) is not rooted and must extract its nutrients from the water. Consequently it must compete with benthic algae and phytoplankton for available nutrients, and benthic productivity, whether algal or of higher macrophytes, may be dependent on nutrient fluxes from the sediments. The macrophytes are also a perennial community and excess net production in one year could allow decomposition to exceed photosynthesis in a subsequent year as we have observed, although we have assumed a single season for our annual input calculations. We cannot evaluate such year to year variability. Decomposition rates and, by inference, nutrient regeneration rates are relatively constant at all depths. Algae may have a competitive advantage in the wave zone in which the non-rooted macrophytes are suppressed, but macrophyte photosynthesis probably predominates at

greater depths. In any case, there would be a plant community absorbing light at all depths until plant growth is limited by light availability.

The rates of benthic aerobic respiration in Lake 18 are the highest so far observed in the Arctic (Table 7), and the rates during the summer are comparable to rates measured in temperate systems. Lake 18 benthic respiration is much higher than observed in Alaskan ponds and lakes (Table 7). When Welch & Kalff (1974) measured respiration in the moss zone of Char Lake (3–19 m; maximum temperature 4 °C) with acrylic chambers it was equivalent to 7.6 mmole C m^{-2} d^{-1} produced, more than twice the rate of other sites examined in Char Lake. However, respiration of the Char Lake moss zone was less than half of the Lake 18 mean value. M. Holoka (Fisheries and Oceans, Winnipeg, unpubl. data) utilized the same chambers employed in this study in temperate, oligotrophic Canadian Shield lakes. He found rates of oxygen consumption in the dark that were approximately half of Lake 18 rates. In Lake 18, winter respiration rates were only 10% of the summer rates. Respiration rates of Lake 18 during the open water season are comparable to those in temperate, eutrophic Lawrence Lake (Table 7). The annual respiration in Lawrence lake is 3 times greater than in Lake 18, but the ice-free period is also approximately 3 times longer. Therefore, in at least some arctic lakes, organic carbon is processed as rapidly as it is in temperate lakes during the open water period.

Summer anaerobic decomposition was 1.6 mmole C m^{-2} d^{-1}, only 4% of the mean aerobic rate (38 mmole C m^{-2} d^{-1}). The only study we could find which measured both aerobic and anaerobic decomposition was that of Jones & Simon (1980). Their work on Blelham Tarn (a temperate lake, Z_{max} = 14 m) showed that 42% of the CO_2 production was aerobically generated; 25% was from methanogenesis, 17% from denitrification and 2% from sulfate reduction. The low rate of anaerobic decomposition during the ice-free season in Lake 18 (compared to temperate lakes, Jones & Simon 1980; Kelly et al. 1984) may be an indirect result of benthic photosynthesis. Benthic photosynthesis will keep the sediment-water interface well oxygenated. The low mean water temperature increases oxygen solubility and causes it to diffuse into the sediments (indicated by the absence of methane until 2 cm into the sediment (Fig. 3). Alternatively both Jones & Simon (1980) and Kelly et al. (1984) only measured anaerobic decomposition in the hypolimnion of temperate lakes where benthic photosynthesis would not be expected to be important. To obtain a comparable data set from temperate lakes, benthic photosynthesis and both aerobic and anaerobic microbial activity in littoral sediments would have to be measured. The oxygen generation at the sediment-water interface by benthic photosynthesis should ensure that most decomposition is achieved near the interface with minimal loss (only 5%) of organic material to sediment burial.

In Lake 18 the open water rates of aerobic benthic respiration approximated the rates of total photosynthesis (Table 7). These measurements by themselves could not have indicated the important role of allochthonous inputs. With the

exception of extremely shallow Alaskan ponds and Lake 18, measurement of total photosynthesis in other lakes in Table 7 consistently exceeded benthic respiration by 50–100%. Although winter respiration, which would tend to balance the carbon budget, is not available for all these lakes, the apparent excess of photosynthesis over benthic respiration in the other lakes in Table 7 would suggest that allochthonous inputs are not as important in these other lakes. Without completed carbon budgets or at least measurements of the net exchange of CO_2 between the lake and the atmosphere, it is not possible to evaluate either the validity of the measurements of the terms in the organic carbon budget or the whole lake balance of photosynthesis and respiration. The measurement of the net flux of CO_2 from the lake to the atmosphere has not yet been made on many lakes, but we suggest that it should be considered in any study where the carbon budget and lake productivity are an issue. In Lake 18 the flux of CO_2 exchange to the atmosphere confirmed the balance indicated by lacustrine measurements of photosynthesis and respiration, and the nitrogen stable isotope measurements confirmed the significant input of allochthonous organic material to the sediments. While these two measurements do not directly enter the carbon budget equation, the former provides the critical information about air-water flux while the latter demonstrates the magnitude of watershed-sediment fluxes. Knowledge of these fluxes helps to constrain the carbon budget for Lake 18 and increases our confidence in the individual estimates of terms of the carbon budget.

In 1979 over one million immature broad whitefish migrated up through counting fences on the Kukjuktuk stream into the system of lakes of which Lake 18 is a member (Chang-Kue & Jessop 1992). Such high fish densities and the high open water rates of photosynthesis and respiration in Lake 18 indicate that arctic lakes can be very productive habitats. Our study has shown Lake 18 to have the highest rates of photosynthesis yet measured in an unperturbed arctic lake. This photosynthesis could support a productive food chain and seasonally high rates of feeding by fish. Our study has also shown the relative importance of benthic photosynthesis (50%), phytoplankton photosynthesis (20%) and allochthonous inputs (30%) to the lake's organic carbon budget. Our results support the findings of Schell (1983) who concluded that allochthonous inputs of carbon were very important contributors to the carbon budgets of arctic freshwater lakes in Alaska. It is possible that the allochthonous inputs may only contribute to the total system respiration, but transport of autochthonously produced carbon to higher trophic levels may be the dominant process supporting the food chain in this lake. The lakes on the Tuktoyaktuk Peninsula are valuable feeding resources sustaining the large populations of broad whitefish in the Mackenzie River and its estuary. Future impact assessment of the shallow lakes of the western Canadian Arctic where oil and gas development is occurring must consider the ecology of the benthic plant community and watershed disturbances which may affect allochthonous inputs as well as the role of the phytoplankton if the productivity of these lakes is to be sustained.

Acknowledgements

This paper is a compilation of information from many sources; we thank the following people for various contributions: C. Anema, M. J. Capel, B. Fallis, D. Fox, A. Furutani, K. Hallard, B. Hauser, S. Himmer, M. Holoka, R. Hunt, M. Lawrence, C. Kelly, H. Kling, D. Mathew, G. McCullough, P. Sandberg, and E. Schindler. The National Museum of Natural Sciences confirmed the macrophyte identifications. We especially thank the staff of the Inuvik Research Laboratory for their help in making this project possible. Critical comments by G. J. Brunskill, P. Campbell, B. Fallis, J. E. Hobbie, D. W. Schindler, H. E. Welch, R. G. Wetzel and three anonymous reviewers greatly improved this manuscript. This work was supported in part by funding from the Northern Oil and Gas Action Plan and by the Canadian National Science and Engineering Research Council grant numbers OGPGP 010 and STRGP 036.

References

Anema C, Hecky RE, Fee EJ, Nernberg D & Guildford S (1990a) Water chemistry of some lakes and channels in the Mackenzie Delta and on the Tuktoyaktuk Peninsula, N.W.T., 1985. Can. Data Rep. Fish. Aquat. Sci. 726: vii + 73 pp

Anema C, Hecky RE, Himmer S & Guildford S (1990b) Water chemistry of some lakes and channels in the Mackenzie Delta and on the Tuktoyaktuk Peninsula, N.W.T., 1986. Can. Data Rep. Fish. Aquat. Sci. 729: vi + 63 pp

Atkinson MJ & Smith SV (1983) C:N:P ratios of benthic marine plants. Limnol. Oceanogr. 28: 568–574

Bodaly RA, Reist JD, Rosenberg DM, McCarthy PJ & Hecky RE (1989) Fish and fisheries of the Mackenzie and Churchill River basins, northern Canada. In: Dodge DP (ed) Proc. International Large River Symp. (pp 128–144) Canadian Department of Fisheries and Oceans

Bond WA & Erickson RN (1982) Preliminary results of a fisheries study of two freshwater lake systems on the Tuktoyaktuk Peninsula, Northwest Territories Can. Department of Fisheries and Oceans. Can. Data Rep. Fish. Aquat. Sci. 348: vi + 62pp

Bond WA & Erickson RN (1985) Life history studies of anadromous coregonid fishes in two lake systems on the Tuktoyaktuk Peninsula, Northwest Territories. Department of Fisheries and Oceans. Can. Tech. Rep. Fish. Aquat. Sci. 1336: vii + 61pp

Bower PM, Kelly CA, Fee EJ, Shearer JA, DeClercq DR & Schindler DW (1987) Simultaneous measurement of primary production by whole-lake and bottle radiocarbon additions. Limnol. Oceanogr. 32: 299–312

Chang-Kue KTJ & Jessop EF (1992) Coregonid migration studies at Kukjuktuk Creek, a coastal drainage on the Tuktoyaktuk Peninsula, Northwest Territories. Department of Fisheries and Oceans. Can. Tech. Rep. Fish. Aquat. Sci. 1811: ix + 112pp

Crusius J & Wanninkhof RH (1990) A gas exchange-wind speed relationship measured on Lake 302N with SF_6. Eos Trans. AGU 71: 1234

Fee EJ (1980) Important factors for estimating annual phytoplankton production in the Experimental Lakes Area. Can. J. Fish. Aquat. Sci. 37: 513–522

Fee EJ (1984) Freshwater Institute primary production model user's guide. Department of Fisheries and Oceans. Can. Tech. Rep. Fish. Aquat. Sci. 1328: v + 36 pp

Fee EJ, Hecky RE, Guildford SJ, Anema C, Mathew D & Hallard K (1988) Phytoplankton

Primary Production and Related Limnological Data for Lakes and Channels in the Mackenzie Delta and Lakes on the Tuktoyaktuk Peninsula, NWT. Department of Fisheries and Oceans. Can. Tech. Rep. Fish. Aquat. Sci. 1614: v + 62 pp

Froelich PH, Klinkhammer GP, Bender ML, Luedtke NA, Heath GR, Cullen D, Dauphin P, Hammond D, Hartman B & Maynard V (1979) Early oxidation of organic matter in pelagic sediments of the eastern equatorial Atlantic: suboxic diagenesis. Geochim. Cosmochim. Acta 45: 1075–1090

Hargrave BT (1969) Epibenthic algal production and community respiration in the sediments of Marion Lake. J. Fish. Res. Board Can. 26: 2003–2036

Hesslein RH (1976) An *in situ* sampler for close interval porewater studies. Limnol. Oceanogr. 21: 912–914

Hesslein RH, Fox DE & Capel MJ (1989) Sulfur, carbon and nitrogen composition of fish from the Mackenzie River Delta Region and other Arctic drainages. Department of Fisheries and Oceans. Can. Data Rep. Fish. Aquat. Sci. 728: iv + 11 pp

Hesslein RH, Capel MJ, Fox DE & Hallard KA (1991) Stable isotopes of sulfur, carbon, and nitrogen as indicators of trophic level and fish migration in the lower Mackenzie River basin, Canada. Can. J. Fish. Aquat. Sci. 48: 2258–2265

Himmelblau DM (1964) Diffusion of dissolved gases in liquids. Chem. Rev. 64: 527–550.

Hobbie JE (1964) Carbon 14 measurements of primary production in two Alaskan lakes. Int. Ver. theor. angew. Limnol. Verh. 15: 360–364

Hobbie JE (1980) Limnology of tundra ponds: Barrow, Alaska. Volume 13 of US/IBP Synthesis series, Dowden, Hutchinson and Ross, Inc., Stroudsburg, Pennsylvania.

Jones JG & Simon BM (1980) Decomposition processes in the profundal region of Blelham Tarn and the Lund tubes. J. Ecol. 68: 493–512

Kalff J & HE Welch (1974) Phytoplankton production in Char Lake, a natural polar lake, and in Meretta Lake, a polluted polar lake, Cornwallis Island, Northwest Territories. J. Fish. Res. Board Can. 31: 621–636

Kelly CA & Rudd JWM (1984) Epilimnetic sulfate reduction and its relationship to lake acidification. Biogeochemistry J. 1: 63–77

Kelly CA, Rudd JWM, Cook RB & Schindler DW (1982) The potential importance of bacterial processes in regulating rate of lake acidification. Limnol. Oceanogr. 27: 868–882

Kelly CA, Rudd JWM, Furutani A & Schindler DW (1984) Effects of lake acidification on rates of organic matter decomposition in sediments. Limnol. Oceanogr. 29: 687–694

Kipphut GW (1978) An investigation of the rates of some physical processes in lake sediments. Ph.D. Thesis, Columbia University, New York, N.Y.

Lawrence MJ, Lacho G & Davies S (1984) A survey of the coastal fishes of the southeastern Beaufort Sea. Department of Fisheries and Oceans. Can. Tech. Rep. Fish. Aquat. Sci. 1220: x + 178 pp

Li YJ & Gregory S (1974) Diffusion of ions in sea water and deep sea sediments. Geochim. Cosmochim. Acta 38: 703–714

Mackay J (1963) The Mackenzie Delta Area, N.W.T. Can, Dept. Mines and Technical Surveys, Geographical Branch. Memoir 8: 202 pp

Miller MC, Hater GR, Spatt P, Westlake P & Yeakel D (1986) Primary production and its control in Toolik Lake, Alaska. Archiv. f. Hydrobiol. Supp. 74: 97–131

Oglesby RT (1977) Relationships of fish yield to lake phytoplankton standing crop, production, and morphoedaphic factors. J. Fish. Res. Board Can. 34: 2271–2279

Pang PC & Nriagu JO (1977) Isotope variations of the nitrogen in Lake Superior. Geochim. Cosmochim. Acta 41: 811–814

Peters KE, Sweeney RE & Kaplan IR (1978) Correlation of carbon and nitrogen stable isotope ratios in sedimentary organic matter. Limnol. Oceanogr. 23: 598–604

Peterson BJ & Fry B (1987) Stable isotopes in ecosystem studies. Ann. Rev. Ecol. Syst. 18: 293–320

Ramlal PS, Anema C, Cummings E, Fee EJ, Guildford SJ, Hallard KA, Hecky RE, Hesslein

RH, Himmer S, Kling H, Mathew D, Nernberg D & Schindler E (1991) Macrophyte and algal studies of some lakes in the Mackenzie Delta and on the Tuktoyaktuk Peninsula 1985–1986. Can. Data Rep. Fish. Aquat. Sci. 839: v + 87 pp

Rudd JWM, Kelly CA, St. Louis VH, Hesslein RH, Furutani A & Holoka MH (1986) Microbial consumption of nitric and sulfuric acids in acidified north temperate lakes. Limnol. Oceanogr. 31: 1267–1280

Schell DM (1983) Carbon-13 and Carbon-14 abundances in Alaskan aquatic organisms: delayed production from peat in Arctic food webs. Science 219: 1068–1071

Schindler DW, Welch HE, Kalff J, Brunskill GH & Kritsch N (1974) Physical and chemical limnology of Char Lake, Cornwallis Island (75 °N lat.). J. Fish. Res. Board Can. 31: 585–607

Sheath RG, Munawar M & Hellebust JA (1975) Phytoplankton biomass composition and primary productivity during the ice-free period in a tundra pond. In: Proc. Circumpolar Conf. Arctic Ecol. (pp III, 21–31) National Research Council, Ottawa

Stainton MP, Capel MJ & Armstrong FAJ (1977) The chemical analysis of freshwater, 2nd ed. Can. Fish. Mar. Serv. Misc. Spec. Publ. 25: 166 pp

Wanninkhof R , Ledwell JR & Broecker WAS (1985) Gas exchange-wind speed relation measured with sulfur hexafluoride on a lake. Science 227: 1224–1226

Welch HE (1974) Metabolic rates of arctic lakes. Limnol. Oceanogr. 19: 65–73

Welch HE & Bergmann MA (1985) Winter respiration of lakes at Saqvaqjuac, N.W.T. Can. J. Fish. Aquat. Sci. 42: 521–528

Welch HE & Kalff J (1974) Benthic photosynthesis and respiration in Char Lake. Can. J. Fish. Aquat. Sci. 31: 609–620

Welch HE, Legault JA & Kling HJ (1989) Phytoplankton, nutrients, and primary production in fertilized and natural lakes at Saqvaqjuac, N.W.T. Can. J. Fish. Aquat. Sci. 46: 90–107

Wetzel RG (1975) Limnology. W.B. Saunders Co., Philadelphia.

Wetzel RG, Rich PH, Miller MC & Allen HL (1972) Metabolism of dissolved and particulate detrital carbon in a temperate hard-water lake. Mem. Ist. Ital. Idrobiol. 29 (suppl.): 185–243

Whalen SC & Cornwell JC (1985) Nitrogen, phosphorus, and organic carbon cycling in an arctic lake. Can. J. Fish. Aquat. Sci. 42: 797–808