

Winter respiration of allochthonous and autochthonous organic carbon in a subarctic clear-water lake

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Abstract

We studied a small subarctic lake to assess the magnitude of winter respiration and the organic carbon (OC) source for this respiration. The concentration and stable isotopic composition ($\delta^{13}\text{C}$) of dissolved inorganic carbon (DIC) accumulating in the lake water under ice was analyzed over one winter (7 months). The DIC concentration increased and the $\delta^{13}\text{C}$ of DIC decreased over time, with the greatest changes at the lake bottom. Winter respiration was 26% of annual respiration in the lake. Keeling plot analysis demonstrated that the $\delta^{13}\text{C}$ of respired DIC varied spatially, high $\delta^{13}\text{C}$ values occurring at shallow (2.5 m, -21.7‰) compared with intermediate (4 m, -25.1‰) and deep (6 m, -27.8‰) locations in the lake. The variation in the $\delta^{13}\text{C}$ of respired DIC was related to the variation in the $\delta^{13}\text{C}$ of the sediments between locations, suggesting that sediment OC supported much of the winter respiration and that the dominant OC source for respiration was OC from benthic algae at shallow locations and settled OC, of predominately terrestrial origin, at deep locations. The respiration of OC from benthic algae constituted 55% of the winter respiration, equaling 54% of the primary production by benthic algae the previous summer. The study indicates the importance of temporal and spatial variation in respiration for the metabolism and net DIC production in unproductive high-latitude lakes; both allochthonous and autochthonous carbon can contribute to winter DIC accumulation and, consequently, to spring CO_2 emissions from lakes.

Recent research has provided strong evidence that most unproductive lakes are net heterotrophic, i.e., that total community respiration exceeds gross photosynthetic carbon fixation (Duarte and Prairie 2005). Net heterotrophy is caused by the import and respiration of terrestrial (allochthonous) organic carbon (OC) (del Giorgio et al. 1999; Karlsson et al. 2007), but the metabolic imbalance may be enhanced by an accompanying negative effect of allochthonous OC on lake primary production (Carpenter et al. 1998; Houser et al. 2003). Respiration often exceeds primary production in the pelagic habitat of unproductive lakes (del Giorgio and Peters 1994). Although few comparative data are available, it is clear that respiration in the sediment could be high and also quantitatively important for total respiration and net CO_2 production in shallow lakes (Kortelainen et al. 2006). However, in clear-water lakes the benthic respiration should be largely supported, and hence offset, by high carbon uptake by benthic algae, causing the benthic habitat to be close to metabolic balance or even net autotrophic in summer (Algesten et al. 2005). The net heterotrophy of clear-water lakes in summer is therefore mainly an effect of high

respiration relative to the CO_2 fixation in the pelagic system (Algesten et al. 2005).

Mineralization in winter is poorly understood and seldom considered in studies of the metabolic balance of lakes. Although metabolic activity is relatively low in winter, this period could be important for the carbon cycling in lakes in regions subject to long winters (Welch and Bergmann 1985). Including the winter period in annual estimates increases the respiration versus carbon fixation ratio of lakes, the greatest relative importance of the winter period being found in lakes at high latitudes and altitudes. High winter CO_2 accumulation and the release of CO_2 during ice breakup in spring has been demonstrated in many lakes receiving a high input of terrestrial OC (Striegl et al. 2001). The magnitude of this process has been related to the concentration of dissolved OC (DOC) in the lakes and, from the stable isotopic composition ($\delta^{13}\text{C}$) of dissolved inorganic carbon (DIC), explained by the mineralization of terrestrial OC in winter (Striegl et al. 2001).

However, clear-water lakes can also exhibit considerable CO_2 accumulation in winter (Kling et al. 1992; Striegl et al. 2001). The source of the OC that supports winter respiration in clear-water lakes is less obvious. Especially in the case of shallow clear-water lakes, in which benthic algae photosynthesize at a high rate in summer (Vadeboncoeur et al. 2003), it could be expected that part of the CO_2 sequestering and buildup of autotrophic biomass in summer could support heterotrophic metabolism the following winter. If that is true, part of the CO_2 emission

Acknowledgments

We thank Thomas Westin for field and laboratory assistance and Anders Olsson and Håkan Wallmark for the stable isotopic analyses. This study was financially supported by the Climate Impacts Research Centre (CIRC), Umeå University, and the Swedish Research Council.

to the atmosphere in spring from clear-water lakes may be derived from the winter respiration of OC produced by benthic algae the previous summer.

We studied a small clear-water subarctic lake to investigate the magnitude and OC support of respiration in winter. We hypothesize that OC produced by benthic algae will be a substantial OC source for respiration and net CO₂ production in winter. We tested the hypothesis by following the concentration and $\delta^{13}\text{C}$ of DIC under the ice during the course of one winter. On the basis of the data gathered, we estimated the $\delta^{13}\text{C}$, rate of respiration, and, by comparison with the $\delta^{13}\text{C}$ of OC sources in the lake, the carbon support for respiration in winter.

Materials and methods

The study was carried out in Lake Alnberga. The lake is small (mean depth 3.2 m, maximum depth 6 m, area 0.055 km²) and is located at 68°19'91"N, 19°09'22"E in the birch forest belt in subarctic northern Sweden. The lake bottom consists of a nearshore region rich in rocks to a depth of approximately 1.5 m, whereas deeper parts consist of soft sediments containing associated epipelagic algae. Macrophytes are not common in the lake.

The lake was sampled from June 2005 to March 2006, every third week during the ice-free period (June–September) and monthly in winter (October 2005–March 2006). The ice thickness was measured on each sampling occasion. Photosynthetically active radiation (PAR) in the water column was measured in the surface water or directly below the ice using an LI-193 spherical quantum sensor (LI-COR Biosciences). DOC, total nitrogen (Tot-N), total phosphorous (Tot-P), and pH were analyzed in water from a composite sample during the ice-free period and from a depth of 2 m over the greatest depth in winter. The composite water sample (10–11 liters) was collected with a tube sampler (0.5 m long, $\phi = 5$ cm) from every 1-m depth interval at three different stations in the lake. The amount of water collected from each layer was proportional to the layer's share of the total lake volume. DOC, Tot-P, and Tot-N were analyzed using standardized methods at the Department of Limnology, Uppsala University, Sweden. The $p\text{CO}_2$ was measured at a depth of 1 m following the method of Jonsson et al. (2003). Water was sampled with a Ruttner sampler (2 liters), and 1,125-mL glass bottles were filled without creating air bubbles, and allowing water to overflow the bottle. Fifty milliliters of headspace gas (He) were equilibrated with lake water by vigorously shaking the bottle for 1 min and after which it was left to stand for one additional minute. The headspace gas was transferred to a plastic syringe and the concentration of CO₂ in the headspace gas was analyzed with a gas chromatograph (CP4900, Varian). The concentration of CO₂ in the water in each bottle was calculated from the concentration of CO₂ in the headspace according to the method of Cole et al. (1994), using Henry's law and the fugacity–pressure relationship presented by Weiss (1974).

The respiration rate and OC sources supporting respiration in winter were estimated from the accumulation of DIC in the lake water under ice during the ice-cover period

between November and March (Welch and Bergmann 1985). Light begins to penetrate the ice when the snow melts in late spring (April–May), so photosynthesis could be high in the lake in the last few weeks before the ice melts; however, this period was not included when calculating respiration rates and OC sources from DIC changes under ice. Samples for the analysis of DIC concentrations and the $\delta^{13}\text{C}$ of the DIC were collected from each 1-m depth interval at shallow (2.5 m), intermediate (4 m), and deep (6 m) locations in the lake with a Ruttner sampler and transferred into 118-mL bottles. The samples were analyzed for DIC concentration and the $\delta^{13}\text{C}$ of the DIC using a headspace equilibration technique (Cole et al. 1994; Miyajima et al. 1995). The bottles were acidified (HCl, pH < 2) and 20 mL of He were added to create a headspace. The bottles were shaken for 1 min and then left to stand for an additional minute. The headspace gas was transferred to evacuated 12-mL exetainers and analyzed for CO₂ concentration and the $\delta^{13}\text{C}$ signature using an ANCA-NT gas purification module and a model 20-20 stable isotope analyzer (Europa Scientific). The results are expressed using the δ notation in per mil (‰) as $\delta^{13}\text{C} = (R_{\text{sample}} : R_{\text{standard}} - 1) \times 1000$, where $R = {}^{13}\text{C} : {}^{12}\text{C}$. The analytical precision of the isotopic analysis was better than 0.3‰. The isotopic composition of the carbon source added on each sampling occasion was estimated from the change in the concentration and the $\delta^{13}\text{C}$ of the lake DIC pool (assuming freeze-out of CO₂; Killawee et al. 1998) in winter using the Keeling plot method (Pataki et al. 2003; Karlsson et al. 2007).

Samples for the analysis of the $\delta^{13}\text{C}$ of lake water particulate organic matter (POM) were collected at the deepest location, and surface sediment (0–1 cm) was collected at depths of 2, 2.5, 3, 4, 5, and 6 m following the method of Karlsson et al. (2003). Artificial rocks in the form of stone cylinders (3 cm high, $\phi = 5$ or 8 cm, $n = 4$) were placed on the lake bottom in June at a depth of 1 m to provide an easily handled substrate for the growth of epilithic algae; the material growing on the cylinders was collected at the end of summer. The solid samples were dried (either freeze-dried or dried at 65°C) and analyzed for $\delta^{13}\text{C}$ using an Europa Scientific carbon and nitrogen analyzer connected to an Europa 20-20 stable isotope analyzer (analytical precision better than 0.3‰).

Primary production in the pelagic region was measured in summer for 4 h at midday according to the standard ¹⁴C incorporation method described by Schindler et al. (1972) and converted to daily whole-lake values following the method of Karlsson et al. (2002). Pelagic respiration was estimated in summer by collecting water from a depth of 1 m and analyzing the change in DIC during incubation in the dark at in situ temperature. Primary production in the soft-bottom benthic habitat in summer was obtained from the change in DIC concentration in transparent and dark plastic tubes, each containing a sediment core and overlying water. A total of 14 sediment cores were collected from depths of 2, 2.5, 3, 4, and 5 m (in triplicate at the shallowest depths) and incubated in the lake at each sampling depth for 24 h. Before and after incubation, a 118-mL water sample was taken from the overlying water

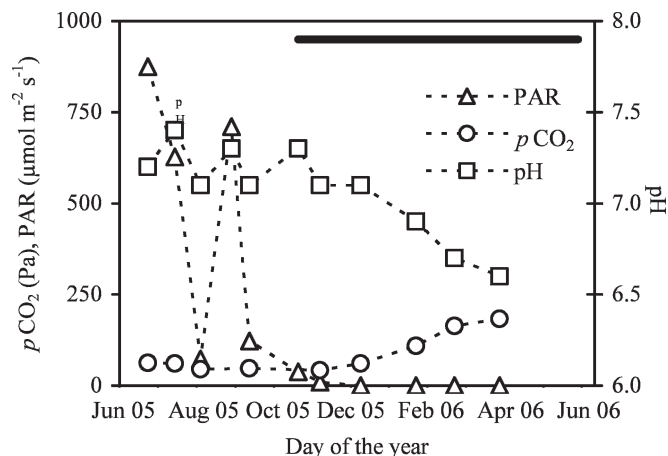


Fig. 1. PAR, $p\text{CO}_2$, and pH from June 2005 to March 2006 in Lake Almberga. The vertical line indicates the extent of the ice cover.

in the tubes, acidified, and analyzed for DIC as described above using a CP4900 gas chromatograph. Sediment respiration in summer was estimated from the DIC increase in dark incubation chambers following the same protocol as described above for benthic primary production. In winter, sediment respiration was measured on two occasions (i.e., November and January) at shallow (2.5 m) and deep (6 m) locations (three replicates per depth). The whole-lake benthic primary production and respiration were calculated using the depth–bottom area relationship of the lake.

Results

Ice formed on the lake in early October, melted partly in mid-October, and then formed a permanent cover in late October 2005, which lasted until late May 2006 (Fig. 1). The ice thickness grew throughout the winter sampling period, from 0.2 m in early November to 1.0 m in late March. The PAR in the lake water decreased to very low values after ice formation (and subsequent snowfall) and was undetectable under ice between November and March (Fig. 1). The DOC concentration (mean \pm 1 SD: $4.1 \pm 0.2 \text{ mg L}^{-1}$, $n = 11$), Tot-N ($156 \pm 26 \text{ mg L}^{-1}$, $n = 10$), and Tot-P ($10.6 \pm 3.5 \text{ µg L}^{-1}$, $n = 7$) displayed small variation over the sampling period. After ice formation in late October, the lake water $p\text{CO}_2$ increased and the pH decreased relative to the values in summer (Fig. 1). The primary production in soft sediment decreased with increasing water depth (Fig. 2). The mean primary production and respiration during the ice-free period were estimated to be, respectively, 10.3 and $191.8 \text{ g C m}^{-2} \text{ d}^{-1}$ in the pelagic habitat and 101.5 and $113.3 \text{ g C m}^{-2} \text{ d}^{-1}$ in the benthic habitat (Table 1). Mean sediment respiration in winter was estimated to be $60.6 \text{ mg C m}^{-2} \text{ d}^{-1}$ (range of all incubations: $34\text{--}76 \text{ mg C m}^{-2} \text{ d}^{-1}$), no differences being found between depths (t -test, $p = 0.658$). The $\delta^{13}\text{C}$ of the epilithic algae at a depth of 1 m was -24.7‰ and the $\delta^{13}\text{C}$ of the pelagic POM was -30.8‰ (Fig. 2). The $\delta^{13}\text{C}$ of the surface sediment decreased (-25.7 to -31.6‰) with increasing depth (Fig. 2).

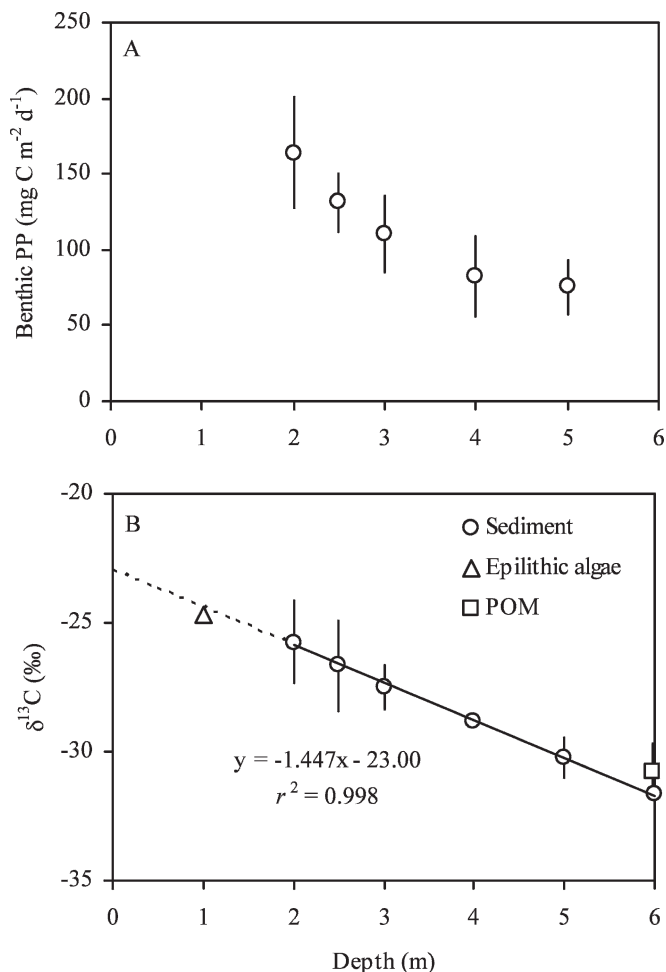


Fig. 2. (A) Benthic primary production (PP) and (B) stable carbon isotopic composition ($\delta^{13}\text{C}$, ‰) of surface sediments, organic matter on rocks incubated in the lake (epilithic algae), and pelagic POM in Lake Almberga. The values represent mean values (\pm 1 SD) for summer 2005. The broken line in B represents the $\delta^{13}\text{C}$ of sediments between depths of 0 and 2 m inferred from the linear change of sediment $\delta^{13}\text{C}$ between depths of 2 and 6 m.

In general, the concentration of DIC increased while the $\delta^{13}\text{C}$ of the DIC decreased under the ice, these changes becoming more pronounced with depth in the water column (Fig. 3). The changes in both the concentration and $\delta^{13}\text{C}$ of the DIC were also more pronounced at deep than at shallow locations in the lake. The total mass of DIC increased over the winter (Fig. 4). From the accumulation of DIC over the winter, total respiration was calculated to be $52.4 \text{ g C m}^{-2} \text{ d}^{-1}$ at shallow, $81.0 \text{ g C m}^{-2} \text{ d}^{-1}$ at intermediate, and $94.6 \text{ g C m}^{-2} \text{ d}^{-1}$ at deep locations. Winter respiration amounted to $16.1 \text{ g m}^{-2} \text{ C}$ for the whole lake.

Keeling plot analysis (Fig. 5) revealed that the $\delta^{13}\text{C}$ of accumulated DIC decreased from shallow (-21.7‰), through intermediate (-25.1‰), to deep locations (-27.8‰) in the lake. The respired DIC was ¹³C enriched compared with pelagic POM, except at the deep locations. The $\delta^{13}\text{C}$ of the respired DIC followed the change in $\delta^{13}\text{C}$ of the surface sediment with increasing depth (Fig. 2) but with enrichment of 3.7–4.1‰.

Table 1. Respiration and primary production in different habitats and on the basis of different OC sources (for winter respiration) in Lake Almerga in summer 2005 and winter 2005–2006. Pelagic winter respiration was calculated as the difference between total (derived from DIC accumulation under ice) and benthic respiration (measured).

	Primary production		Respiration			
	Summer		Summer		Winter	
	mg C m ⁻² d ⁻¹	g C season ⁻¹	mg C m ⁻² d ⁻¹	g C season ⁻¹	mg C m ⁻² d ⁻¹	g C season ⁻¹
Habitat						
Pelagic	10.3	1.6	191.8	29.2	(15.3)	(3.2)
Benthic	101.5	15.4	113.3	17.2	60.6	12.9
Total	111.8	17.0	305.1	46.4	75.9	16.1
OC source						
Pelagic OM					33.1	7.0
Benthic algae					42.8	9.1

Discussion

The large changes in DIC, $p\text{CO}_2$, and pH under the ice indicate significant heterotrophic metabolic activity in the lake in winter. PAR was absent from the lake water during the winter sampling period, implying negligible photosynthetic activity and that the DIC accumulation over time reflected the heterotrophic respiration under ice. The respiration in winter was too low to cause anaerobic conditions in the water column, so methane was not found in the water during the sampling period (Ask unpubl. data). We therefore assume that aerobic heterotrophic activity dominated the lake in winter. Groundwater could also contribute to the accumulation of DIC in winter. However, the variation in $\delta^{13}\text{C}$ across sampling depths and locations is evidence of stable conditions and low input of groundwater (high input of groundwater would have resulted in similar $\delta^{13}\text{C}$ values for accumulated DIC across the lake). In fact, although pelagic respiration was not measured in winter, the estimated sediment respiration alone accounted for most (i.e., 80%; see Table 1) of the winter DIC accumulation in the lake.

The accumulation and $\delta^{13}\text{C}$ of DIC varied between depths, implying spatial variation in the source and magnitude of respiration. The higher accumulations at deep compared with shallow locations could be due to the differences in the depth of the water column, enabling higher total pelagic respiration at deep locations. The isotopic data suggest that much of the respiration was based on benthic OC sources. The $\delta^{13}\text{C}$ of respired carbon (Fig. 5) was clearly enriched compared with that of pelagic POM, especially at shallow locations, and was more similar to that of surface sediments (Fig. 2). The $\delta^{13}\text{C}$ of respired carbon at the shallow location was also similar to the $\delta^{13}\text{C}$ of the respired DIC (-23.5%) in shallow sediments in summer 2005 (Ask unpubl. data). However, from the $\delta^{13}\text{C}$ data alone we cannot determine whether the respiration of benthic OC occurred in the sediments or in the water column. The estimated sediment respiration occurring during incubations in winter (Table 1) was sufficient to account for the DIC accumulation under ice at shallow locations and 64% of the DIC accumulation at deep locations. Pelagic respiration was likely significant at deep

locations, but it is impossible to distinguish between respiration in different habitats at this site since the $\delta^{13}\text{C}$ values are similar for benthic and pelagic OC at deep locations (Fig. 2). For the whole lake, however, the estimated benthic respiration suggests that pelagic respiration only contributed approximately 20% of the total winter respiration (Table 1).

Even assuming that the respiration was completely based on sediment OC, the $\delta^{13}\text{C}$ of the respired carbon would still be approximately 4‰ enriched compared with the $\delta^{13}\text{C}$ of the bulk sediment OC. The ^{13}C fractionation during respiration has been reported to be relatively low (Hullar et al. 1996). The differences between respired carbon and sediment OC found in our study were likely mainly due to the preferential degradation of a ^{13}C -enriched fraction of the sediment organic matter (Lehmann et al. 2002). The sediments are composed of settled pelagic OC and of OC generated by benthic algae, and the relative importance of these sources changes with depth. The high $\delta^{13}\text{C}$ in the shallow rather than deep sediments reflects the decreased production of ^{13}C -enriched OC by benthic algae (Fig. 2) and the increased settling of pelagic, ^{13}C -depleted OC with depth (Karlsson and Byström 2005). Thus, the $\delta^{13}\text{C}$ of sediment should approach the $\delta^{13}\text{C}$ of OC from benthic algae at shallow depths. On the basis of the y -axis intercept of the $\delta^{13}\text{C}$ -depth relationship (Fig. 2) of the sediment, the $\delta^{13}\text{C}$ of benthic algae should be approximately -23.0% . The $\delta^{13}\text{C}$ of OC (-24.2%) accumulated on rocks at a depth of 1 m was slightly ^{13}C enriched compared with that of shallow bulk surface sediment but not as high as -23.0% . However, epilithic algae growing on rocks probably discriminate more strongly against ^{13}C than do faster-growing epipelagic algae (Goericke et al. 1994; Hansson and Tranvik 2003; Vadeboncoeur et al. 2003), and the OC on the rocks may also contain a fraction of settled pelagic OC, suggesting that the $\delta^{13}\text{C}$ of epilithic algae in the lake should be higher than the $\delta^{13}\text{C}$ of epipelagic algae recorded in the lake. Furthermore, the $\delta^{13}\text{C}$ of littoral zoobenthos (*Gammarus lacustris*) was as high as -21.6% in summer 2005 (Karlsson unpubl. data), suggesting a food source $\delta^{13}\text{C}$ of approximately -22.0% . Altogether, the data suggest that the $\delta^{13}\text{C}$ of epipelagic algae in Lake Almerga is in the -22.0% to -23.0% range and that the relatively high $\delta^{13}\text{C}$

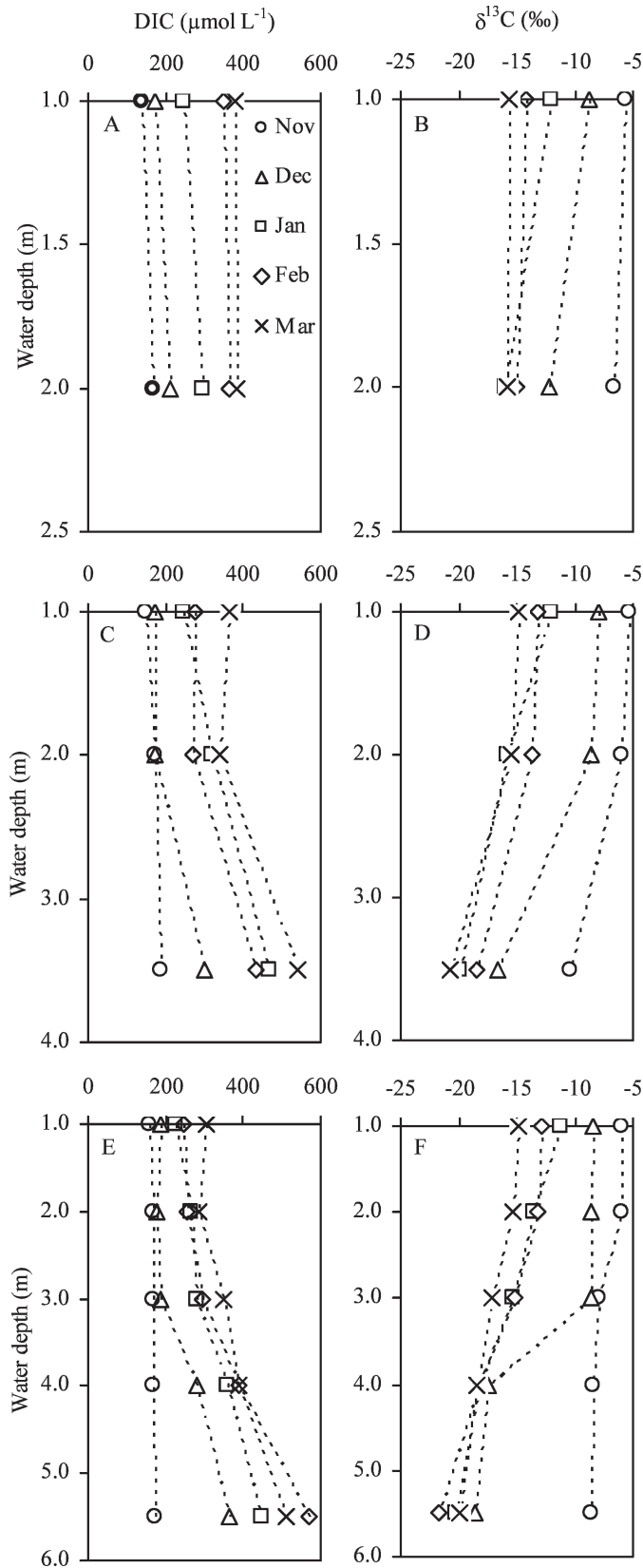


Fig. 3. Concentration and stable isotopic composition ($\delta^{13}\text{C}$) at different water depths at shallow (A and B), intermediate (C and D), and deep (E and F) parts of Lake Almb erga during winter 2005 to 2006.

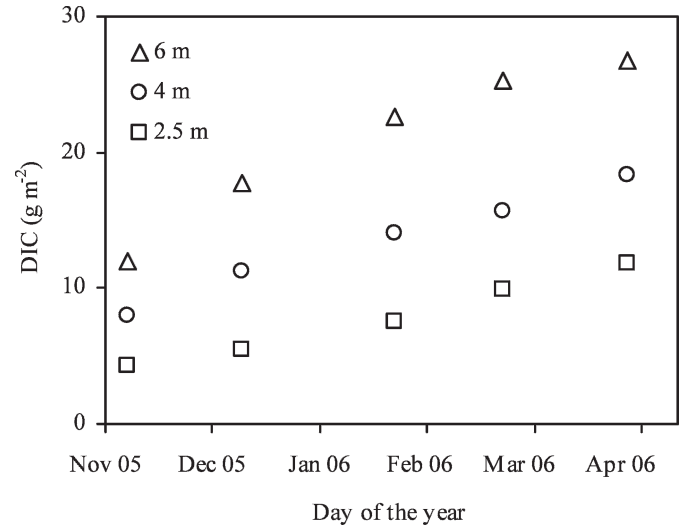


Fig. 4. Total mass of DIC at shallow, intermediate, and deep parts of Lake Almb erga during winter 2005 to 2006.

of respired carbon reflects the preferential respiration of OC from benthic algae in sediments. Assuming that respiration at shallow depths is based on OC generated by benthic algae suggests a fractionation of between 0.3‰ and 1.2‰ between respired CO_2 and the OC source, which is similar to experimentally derived values (Hullar et al. 1996).

A two-source mixing model, assuming a $\delta^{13}\text{C}$ of benthic algae of -22.5‰ , that the $\delta^{13}\text{C}$ of POM reflects the $\delta^{13}\text{C}$ of respired pelagic OC (Karlsson 2007), and a ^{13}C enrichment of 0.8‰ in respired carbon, indicates that OC from benthic algae accounted for 58% and 26% of winter respiration at intermediate and deep locations, respectively. This suggests that the winter respiration of OC from benthic algae corresponds to a rather similar fraction of summer primary production by benthic algae (Fig. 2) at shallow (50%), intermediate (70%), and deep (50%) locations. In total, 55% of winter respiration was supported by OC generated by benthic algae and this respiration equaled 54% of the benthic primary production of the previous summer (Table 1). Considering the low pelagic primary production (Table 1), it is clear that the winter respiration not supported by benthic primary production must be predominately supported by allochthonous OC.

The estimated winter respiration equaled 35% of the respiration (pelagic + benthic) in the lake in summer 2005 and 26% of the annual respiration in the lake (Table 1). On an annual basis, both the pelagic and benthic habitats were net heterotrophic (Table 1). However, the data suggest that the habitat that contributes the most to whole-lake net heterotrophy and net CO_2 production changes over the season. In summer, the benthic habitat is more or less in metabolic balance while the pelagic habitat is highly net heterotrophic and responsible for most of the net CO_2 production in the lake (Table 1). In winter, however, the data suggest that net CO_2 production mainly takes place in the benthic habitat. This seasonal difference could be attributed to the different physical structures of the two

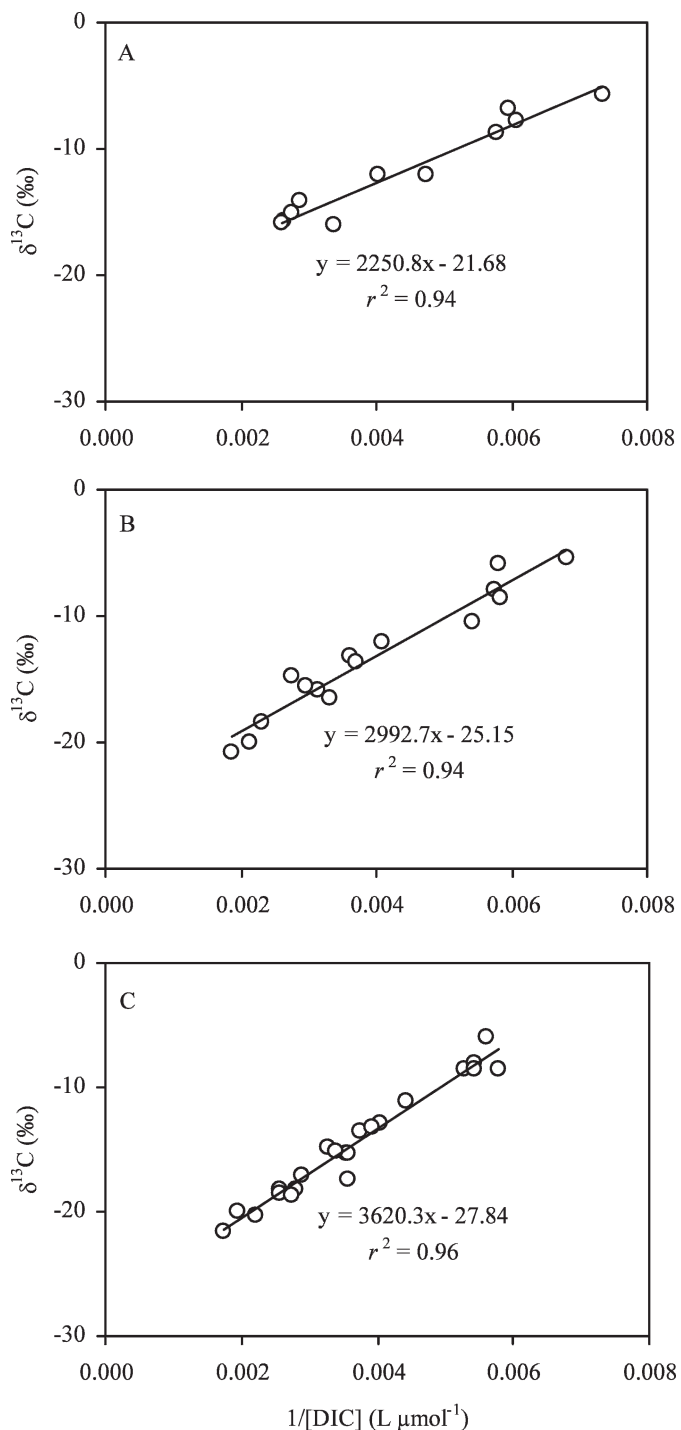


Fig. 5. Keeling plots showing the $\delta^{13}\text{C}$ of DIC plotted against the inverse of the concentration of DIC ($1/[\text{DIC}]$) at (A) shallow, (B) intermediate, and (C) deep locations in Lake Almerga during winter 2005 to 2006. In winter, the respiration of organic carbon adds CO_2 to the background DIC, increasing $[\text{DIC}]$ and changing the $\delta^{13}\text{C}$ of the DIC pool. When respired CO_2 is added to background DIC, a linear relationship exists between $1/[\text{DIC}]$ and $\delta^{13}\text{C}$, with an intercept that corresponds to the isotopic composition of respired CO_2 (Pataki et al. 2003).

habitats, the respiration in the pelagic habitat being dependent on a continuous OC supply, whereas the respiration in the benthic habitat could be sustained, although at lower rates, by the OC pool accumulated in the previous summer period.

These results are important for understanding the carbon cycling in clear-water lake ecosystems. The data show that the winter respiration accounted for a considerable proportion of the annual carbon budget of the lake. The total winter respiration in Lake Almerga was slightly lower than estimated values for similar lakes in North America (Welch and Bergmann 1985) but agreed with estimates of $p\text{CO}_2$ under ice (Striegl et al. 2001; Kortelainen et al. 2006) in terms of both winter accumulation rates and their potential relative importance for annual net CO_2 production and emissions. Furthermore, the data show that much of the benthic primary production in Lake Almerga was respired in winter. Thus, high DIC accumulation in winter and subsequent CO_2 evasion to the atmosphere in spring do not necessarily only result from the decomposition of allochthonous OC, but could largely be generated by the decomposition of autochthonous OC in clear-water lakes.

References

- ALGESTEN, G., S. SOBEK, A. K. BERGSTRÖM, A. JONSSON, L. J. TRANVIK, AND M. JANSSON. 2005. Contribution of sediment respiration to summer CO_2 emission from low productive boreal and subarctic lakes. *Microb. Ecol.* **50**: 529–535.
- CARPENTER, S. R., J. J. COLE, J. F. KITCHELL, AND M. L. PACE. 1998. Impact of dissolved organic carbon, phosphorus, and grazing on phytoplankton biomass and production in experimental lakes. *Limnol. Oceanogr.* **43**: 73–80.
- COLE, J. J., N. F. CARACO, G. W. KLING, AND T. K. KRATZ. 1994. Carbon-dioxide supersaturation in the surface waters of lakes. *Science* **265**: 1568–1570.
- DEL GIORGIO, P. A., J. J. COLE, N. F. CARACO, AND R. H. PETERS. 1999. Linking planktonic biomass and metabolism to net gas fluxes in northern temperate lakes. *Ecology* **80**: 1422–1431.
- , AND R. H. PETERS. 1994. Patterns in planktonic P-R ratios in lakes—influence of lake trophic and dissolved organic carbon. *Limnol. Oceanogr.* **39**: 772–787.
- DUARTE, C. M., AND Y. T. PRAIRIE. 2005. Prevalence of heterotrophy and atmospheric CO_2 emissions from aquatic ecosystems. *Ecosystems* **8**: 862–870.
- GOERICKE, R., J. P. MONTOYA, AND B. FRY. 1994. Physiology of isotopic fractionation in algae and cyanobacteria, p. 187–221. *In* K. Lajtha and R. H. Michener [eds.], *Stable isotopes in ecology and environmental science*. Blackwell.
- HANSSON, L. A., AND L. J. TRANVIK. 2003. Food webs in sub-Antarctic lakes: A stable isotope approach. *Polar Biol.* **26**: 783–788.
- HOUSER, J. N., D. L. BADE, J. J. COLE, AND M. L. PACE. 2003. The dual influences of dissolved organic carbon on hypolimnetic metabolism: Organic substrate and photosynthetic reduction. *Biogeochemistry* **64**: 247–269.
- HULLAR, M. A. J., B. FRY, B. J. PETERSON, AND R. T. WRIGHT. 1996. Microbial utilization of estuarine dissolved organic carbon: A stable isotope tracer approach tested by mass balance. *Appl. Environ. Microbiol.* **62**: 2489–2493.
- JONSSON, A., J. KARLSSON, AND M. JANSSON. 2003. Sources of carbon dioxide supersaturation in clearwater and humic lakes in northern Sweden. *Ecosystems* **6**: 224–235.

- KARLSSON, J. 2007. Different carbon support for community respiration and secondary production in unproductive lakes. *Oikos* **116**: 1691–1696.
- , AND P. BYSTRÖM. 2005. Littoral energy mobilization dominates energy supply for top consumers in subarctic lakes. *Limnol. Oceanogr.* **50**: 538–543.
- , M. JANSSON, AND A. JONSSON. 2002. Similar relationships between pelagic primary and bacterial production in clear-water and humic lakes. *Ecology* **83**: 2902–2910.
- , ———, AND ———. 2007. Respiration of allochthonous organic carbon in unproductive forest lakes determined by the Keeling plot method. *Limnol. Oceanogr.* **52**: 603–608.
- , A. JONSSON, M. MEILI, AND M. JANSSON. 2003. Control of zooplankton dependence on allochthonous organic carbon in humic and clear-water lakes in northern Sweden. *Limnol. Oceanogr.* **48**: 269–276.
- KILLAWEE, J. A., I. J. FAIRCHILD, J. L. TISON, L. JANSSENS, AND R. LORRAIN. 1998. Segregation of solutes and gases in experimental freezing of dilute solutions: Implications for natural glacial systems. *Geochim. Cosmochim. Acta* **62**: 3637–3655.
- KLING, G. W., G. W. KIPPHUT, AND M. C. MILLER. 1992. The flux of CO₂ and CH₄ from lakes and rivers in Arctic Alaska. *Hydrobiologia* **240**: 23–36.
- KORTELAINEN, P., AND OTHERS. 2006. Sediment respiration and lake trophic state are important predictors of large CO₂ evasion from small boreal lakes. *Global Change Biol.* **12**: 1554–1567.
- LEHMANN, M. F., S. M. BERNASCONI, A. BARBIERI, AND J. A. MCKENZIE. 2002. Preservation of organic matter and alteration of its carbon and nitrogen isotope composition during simulated and in situ early sedimentary diagenesis. *Geochim. Cosmochim. Acta* **66**: 3573–3584.
- MIYAJIMA, T., Y. YAMADA, Y. T. HANBA, K. YOSHII, T. KOITABASHI, AND E. WADA. 1995. Determining the stable-isotope ratio of total dissolved inorganic carbon in lake water by GC/C/IRMS. *Limnol. Oceanogr.* **40**: 994–1000.
- PATAKI, D. E., AND OTHERS. 2003. The application and interpretation of Keeling plots in terrestrial carbon cycle research. *Global Biogeochem. Cycles* **17**: 1022, doi:10.1029/2001GB001850.
- SCHINDLER, D. W., R. V. SCHMIDT, AND R. A. REID. 1972. Acidification and bubbling as an alternative to filtration in determining phytoplankton production by the ¹⁴C method. *J. Fish. Res. Board Can.* **29**: 1627–1631.
- STRIEGL, R. G., P. KORTELAINEN, J. P. CHANTON, K. P. WICKLAND, G. C. BUGNA, AND M. RANTAKARI. 2001. Carbon dioxide partial pressure and ¹³C content of north temperate and boreal lakes at spring ice melt. *Limnol. Oceanogr.* **46**: 941–945.
- VADEBONCOEUR, Y., E. JEPPESEN, M. J. VANDER ZANDEN, H. H. SCHIERUP, K. CHRISTOFFERSEN, AND D. M. LODGE. 2003. From Greenland to green lakes: Cultural eutrophication and the loss of benthic pathways in lakes. *Limnol. Oceanogr.* **48**: 1408–1418.
- WEISS, R. F. 1974. Carbon dioxide in water and seawater: The solubility of a non-ideal gas. *Mar. Chem.* **2**: 203–215.
- WELCH, H. E., AND M. A. BERGMANN. 1985. Winter respiration of lakes at Saqvaquac, N.W.T. *Can. J. Fish. Aquat. Sci.* **42**: 521–528.

Received: 15 October 2007

Accepted: 23 January 2008

Amended: 1 February 2008