

Whole-lake mineralization of allochthonous and autochthonous organic carbon in a large humic lake (Örträsket, N. Sweden)

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Abstract

Organic carbon mineralization was studied in a large humic lake (Lake Örträsket) in northern Sweden during a well-defined summer stratification period following high water flow during snowmelt. Several independent methods including plankton counts, measurements of bacterioplankton and phytoplankton production, stable isotope monitoring, sediment trapping, and mass balance calculations were used. Total organic carbon mineralization showed a summer mean of $0.3 \text{ g C m}^{-2} \text{ d}^{-1}$ and was partitioned about equally between water and sediment. In the water column, organic matter was mineralized by bacteria (60%) and protozoan and metazoan zooplankton (30%), as well as by photooxidation (10%). Most of the mineralized organic carbon was of allochthonous origin. Primary production in the lake contributed at most 5% of the total organic carbon input and about 20% of the total organic carbon mineralization. Total carbon mineralization in the epilimnion and metalimnion agreed well with an estimate of CO_2 evasion from the stratified lake, while CO_2 accumulation in the hypolimnion matched the O_2 consumption and resulted in a very negative $\delta^{13}\text{C}$ of DIC before autumn overturn (-23%). Isotopic compositions of DIC and POC confirmed the dominant influence of terrestrial organic input on the cycling of both organic and inorganic carbon in the lake.

Organic carbon is supplied to lakes by primary production in the lake (autochthonous carbon) or by input from the catchment (allochthonous carbon). The relative importance of autochthonous versus allochthonous carbon is highly variable. In eutrophic lakes, most organic carbon is likely supplied by primary production in the lake. Part of this autochthonous production is transferred to food chains and converted to new biomass, and the rest is lost by respiration, outlet export, or long-term burial in sediments. Whole-lake carbon fixation may exceed losses, and the lake can be a net sink of CO_2 . Oligotrophic lakes, on the other hand, are often supersaturated with CO_2 relative to the water-atmosphere equilibrium (Cole et al. 1994; del Giorgio et al. 1997), and are therefore sources of CO_2 to the atmosphere (Hope et al. 1996). Supersaturation has been explained by respiration of allochthonous carbon, which adds to the respiration of small amounts of autochthonous carbon (del Giorgio et al. 1997). In humic lakes, the input of allochthonous dissolved organic

carbon (DOC) is considerably higher than in clearwater oligotrophic lakes, and it can replace autochthonous carbon as the dominant energy source of secondary production and be the main carbon source for CO_2 production (Riera et al. 1999). Although most of the allochthonous organic carbon is regarded as recalcitrant, with only 1–10% being readily used and degraded by bacteria (Moran and Hodson 1990), there are many indications that allochthonous organic carbon dominates not only the input but also the biological carbon cycling in humic lakes (Hessen 1992; Meili et al. 1993; Jansson et al. 1999).

Much of the evidence for the role of allochthonous carbon is either from small-scale experimental studies on bacterial degradation of humic compounds (Moran and Hodson 1990; Leff and Meyer 1991) or from compilations of data sets addressing whole-lake water chemistry, primary production and microbial activity (Cole et al. 1988; del Giorgio et al. 1997). Detailed and comprehensive studies of the partitioning and fate of allochthonous versus autochthonous carbon in whole-lake ecosystems with a high input of humic compounds are rare. The present study was made with the aims of elucidating the mineralization of organic carbon from various sources and by different processes in a deep humic lake during the period of summer stratification and of comparing the biotic turnover within the lake with the total flux of organic matter through the lake.

Methods

Study area—Lake Örträsket in northern Sweden ($64^\circ 10' \text{N}$, $18^\circ 55' \text{E}$) is the only lake along the main course

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Acknowledgements

We thank Lars-Inge Karlsson, Raul Figueroa, Erik Lundberg, Katarina Vrede, Peter Blomqvist, and Ulrika Stensdotter-Blomberg for their help through various stages of this work. Carbon isotope ratios were analyzed by Chris Tholke and staff at The Ecosystems Center, Marine Biological Laboratory, Woods Hole, USA. The Swedish Natural Science Research Council supported this investigation financially.

Table 1. Physical and chemical characteristics of epilimnion (E), metalimnion (M), and hypolimnion (H) during summer stratification in 1994. For each stratum, the average thickness (*Z*), surface area (area), water volume (vol), and water temperature (temp) are given, along with selected chemical parameters. Abbreviations: total nitrogen (TN), total phosphorus (TP). Mean values ($n = 7$) are for the investigation period of 16 June–08 September 1994.

	<i>Z</i> (m)	Area (km ²)	Vol (m ³ 10 ⁶)	Temp (°C)	DOC (μM)	POC (μM)	TN (μM)	TP (μM)	pH
E	8	7.3	57	14.8	775	77	26	0.68	6.6
M	9	5.8	51	9.3	792	57	26	0.64	6.5
H	15	4.0	59	6.5	808	60	28	0.71	6.2

of a nonregulated forest river, the River Öre (annual mean flow 35 m³ s⁻¹). The catchment is mostly covered by coniferous forests (65%) and mires (20%), and lakes cover 3.5% of the catchment area. Only small areas are used for agriculture. The lake has mean and maximum depths of 23 and 64 m, respectively, and a theoretical mean water residence time of 3 months (Jonsson and Jansson 1997). Selected physical and chemical characteristics are presented in Table 1.

Sampling and analyses—The study period of 16 June–8 September 1994 was selected to represent the period of stable thermal stratification. Volume-weighted composite lake water samples were collected biweekly during the study period from the epilimnion, metalimnion, and hypolimnion, respectively, according to Jansson et al. (1999). Water was collected from the major inlets (River Örän and River Vargån) and the outlet (River Öre) on the same occasions as from the lake. Samples were analyzed for DOC according to Jonsson and Jansson (1997). The concentration of particulate organic carbon (POC) in the different waters was not analyzed in 1994. Therefore, POC was estimated from analyses of particulate nitrogen (PN ≥ 0.45 μm) concentrations from 1994 (not shown) using the mean C:N mass ratio of 17:1 (± 3 , 95% confidence interval) determined for particulate matter collected on preignited GF/F-filters in the lake in summer 1995 (Bergström unpubl. data). This ratio is somewhat higher than for settling particles in the lake (15:1 by mass, Jonsson 1997), possibly reflecting a larger share of more degraded material in the total lake water particulate

organic matter (POM) pool. Dissolved inorganic carbon (DIC) was analyzed in water samples collected at a central station in the lake. Samples were taken with a Ruttner sampler on five occasions (16 June, 15 July, 28 July, 10 August, and 8 September) from the middle of the epilimnion, the upper hypolimnion (2–5 m below the metalimnion), and the lower hypolimnion (1–2 m above the sediment). DIC samples were transferred with minimal air contact into tightly capped 250-ml glass bottles and preserved with HgCl₂ (final conc. 0.2 g HgCl₂ L⁻¹). DIC concentrations were quantified during stable isotope analysis (*see below*). Concentration profiles of dissolved oxygen (DO) were measured at the same site and on the same occasions as DIC (*cf.* above) with a portable combined oxygen and temperature meter (WTW OXI-196). DO measurements were made every other meter, with 1-m intervals close to the water surface and sediment.

Subsamples were taken from the volume-weighted composite samples for analyses of bacterial production (³H-leucine incorporation), bacterial numbers (acridine orange direct counting technique [AODC]) and biomass; species compositions and biomasses of phytoplankton, protozoan, and metazooplankton; and chlorophyll *a* concentrations according to Jansson et al. (1999). Net primary production (NPP) could be estimated by multiplying the autotrophic plankton biomass determined in 1994 with the ratio between NPP (H¹⁴CO₃ uptake) and autotrophic plankton biomass measured in 1996 (Jansson et al. 1999), since biomasses and species compositions of autotrophic plankton were similar in 1994 and 1996 (Blomqvist, unpubl. data, Table 2). This P:B ratio (average 0.81 ± 0.36 , 95% confidence interval) was used to calculate NPP in the lake water volume in the 0–4-m depth interval (including the whole photic volume). For a direct comparison with bacterial production in the epilimnion, calculated primary production was expressed per epilimnion volume or area.

Settling particulate matter was collected five times using 8–12 sediment trap stations as described in Jonsson and Jansson (1997). Trap-collected material was analyzed for total particulate matter (*ibid.*) and organic carbon, which was analyzed at Umeå Marine Research Center (Sweden) according to standard methods using a Carlo Erba (1106) elemental analyzer.

Lake carbon balance—An organic carbon mass balance was calculated based on monitoring data, including riverine

Table 2. Epilimnetic summer mean biomasses (μg C L⁻¹) of bacterioplankton, heterotrophic and mixotrophic flagellates (het + mix), autotrophic plankton (auto), ciliated protozoans (ciliates), and metazooplankton (metazoo) in 1999 ($n = 9$), 1995 ($n = 8$), and 1996 ($n = 6$). The concentrations (μg C L⁻¹) of POC (1994, ≥ 0.45 μm; and 1995, ≥ 0.7 μm; *see Methods*) and TOC in the epilimnion are included for comparison. Ranges are given within parentheses.

	1994	1995	1996
Bacteria	62 (43–91)	42 (24–66)	18 (11–35)
Het + Mix	10 (2–19)	6 (1–11)	6 (4–9)
Auto	11 (2–45)	9 (5–13)	10 (3–31)
Ciliates	2 (0–9)*	20 (10–41)	—
Metazoo	6 (0.3–17)	4 (0.3–9)	—
POC	920 (390–1270)	530 (390–740)	—
TOC	10,200 (9,200–11,400)	10,900 (10,000–12,300)	—

* Only large ciliates (>50 μm).

Table 3. Values used for the calculation of carbon mineralization by heterotrophic organisms. Values represent assumed summer means. Values in parentheses represent upper and lower extremes.

	Values	Reference
Bacterial G.E.	28% (20%–36%)*	means, Wikner et al. 1999; extremes, del Giorgio and Cole 1998
Flagellate G.E.	30% (20%–40%)*	Straile 1997
Ciliate G.E.	30% (20%–40%)*	Straile 1997
Metazooplankton G.E.	20% (15%–40%)*	Straile 1997
PDOC excretion	31% (16%–32%)†	Arvola et al. 1996
RQ value	Set to 1	

* Quartiles.

† Range.

input via the two major inlets and diffuse inlets, changes in the lake water content, the output via the outlet of the lake, and settling determined by sediment traps.

Calculations were made as described in Jonsson and Jansson (1997). Retention of carbon in the lake was calculated as the difference between riverine inflow and outflow. Lake water pools of DOC and POC were calculated from the volume-weighted concentration in the different strata and from the volume of each stratum.

Settling of organic carbon was calculated by multiplying the average settling rate in the traps ($212 \pm 33 \text{ mg C m}^{-2} \text{ d}^{-1}$, 95% confidence interval, $n = 54$) with the whole-lake surface area. The possible differences in sedimentation at different water depths were accounted for in this calculation, since traps were located close to the bottom at different depths along and across the whole lake basin (cf. Jonsson and Jansson 1997).

Mineralization—In order to use available data sets to account for the most important processes contributing to the mineralization of organic matter, assumptions and conversions presented in Table 3 were made, most of which were based on other studies in the same and similar systems. Pelagic mineralization of organic carbon was quantified by assessing both abiotic mineralization through photooxidation and biotic mineralization through respiration by bacteria, flagellates, ciliates, and metazoan zooplankton.

Consumption of DO in the hypolimnion was used as an independent estimate of the total respiration (pelagic + benthic) in the hypolimnion, in addition to the accumulation of DIC. Calculations were based on the change of the arithmetic mean concentrations of the upper and the lower hypolimnion over the study period.

Bacterial respiration was calculated from the measured bacterial production in 1994 using the median bacterial growth efficiency (B.G.E.) of 28% (Table 3) determined in Lake Örräsket during 1994–1996 (Wikner et al. 1999). Respiration by phagotrophic flagellates in the epilimnion was estimated from bacterial grazing experiments (using fluorescent microspheres) conducted in the epilimnion of Lake Örräsket during the summers of 1995–1997 (Isaksson et al. 1999; Bergström unpubl. data). An average clearance rate of $1.4 \text{ nl flagellate}^{-1} \text{ h}^{-1}$ ($\pm 0.4 \text{ nl flagellate}^{-1} \text{ h}^{-1}$, 95% confidence interval) was used for both heterotrophic and mixotrophic flagellates. Clearance was estimated by multiplying clearance rates by the phagotrophic flagellate numbers, and ingestion of carbon was estimated by multiplying clearance

with ambient bacterial biomasses. Respiration by flagellates was calculated by using a G.E. of 30% (Table 3). Flagellate respiration in the metalimnion and the hypolimnion was estimated from bacterial respiration in these strata assuming the same ratio between bacterial and flagellate respiration as in epilimnion water.

The epilimnetic ciliate community was not fully counted in 1994 (only large ciliates, $>50 \mu\text{m}$), and carbon ingestion by ciliates was therefore calculated by assuming a similar ciliate community as in 1995, when all ciliates were counted. Clearance rates of $30 \text{ nl ciliate}^{-1} \text{ h}^{-1}$ (Simek et al. 1996) and $105 \text{ nl ciliate}^{-1} \text{ h}^{-1}$ (Stabell 1996) for the phytoplankton and flagellate grazing ciliates (mainly prostomatida) and the bacterial grazing ciliates (mainly oligotricha) were used, respectively. Clearance was obtained by multiplying clearance rates with the number of the respective ciliate type. Ingestion was calculated by multiplying clearance with the biomasses of flagellates and phytoplankton (for prostomatida) and bacteria (for oligotricha), respectively. Ciliate ingestion in the metalimnion and the hypolimnion was calculated assuming that all net production by flagellates in these strata was ingested by ciliates. Ciliate respiration was calculated using a G.E. of 30% (Table 3). Metazoan zooplankton respiration in the different strata was calculated assuming they consumed all ciliate net production and by using a G.E. of 20% (Table 3). Grazing on flagellates by metazoans was thus assumed to be negligible, since the biomass of metazoans was much lower than that of ciliates (Table 2).

Photoformation of DIC was calculated from the experimental results of Bertilsson et al. (1999), using water from five stations in the River Öre, including the outlet of Lake Örräsket. Measured photooxidation rates were found to be well correlated to the DOC concentration ($r_{\text{adj}}^2 = 0.95$, $p = 0.003$, DOC concentration varied between 7.2 and 13.8 mg L^{-1} in the experiment). This relationship was used to estimate photooxidation rates from measured epilimnetic DOC concentrations (8.7–10.3 mg L^{-1}) by assuming that the photooxidation rate was linearly related to the irradiance of UVA. Daily mean UVA radiation was estimated to be 10% of the PAR radiation measured at the Umeå Marine Research Center, about 100 km east of Lake Örräsket. Light attenuation was calculated according to Scully and Lean (1994). Photooxidation was calculated for the 0–1-m water volume, below which UVA radiation is less than 0.07% of the surface radiation.

Calculations of pelagic mineralization suffer from uncertainties due to ranges in, for example, possible growth effi-

Table 4. Mass balance of organic carbon (g C m^{-2}) during the investigation period (84 d). All values are normalized to the lake surface area: Lake water pool on 16 June 1994 (pool_0), lake water pool on 8 September 1994 (pool_{84}), change in lake water pool from day 0 to day 84 (ΔPool), inlet input (input_i), outlet output (output) and retention (ret), primary production input (input_{pp}) including POC and DOC, apparent loss (loss) of organic carbon from the water column by sedimentation and mineralization calculated by subtracting retention and input_{pp} from Δpool . Settling flux (SF), measured with traps. Pelagic mineralization (PM) was calculated as the difference between apparent loss and settling flux.

	Pool_0	Pool_{84}	ΔPool	Input_i	Output	Ret	Input_{pp}	Loss	SF	PM
DOC	219	206	-13	108	114	-6	1.1	8	(≈ 0)	8
POC	26.3	11.6	-14.7	12.3	9.7	2.6	3.6	21	18	3
TOC	245	218	-28	120	124	-4	4.7	29	18	11

ciencies of different types of organisms and the magnitude of phytoplankton exudation (PDOOC). To obtain a measure of how such uncertainties might affect the estimates of mineralization, calculations were made based on the means as well as the upper and lower extremes given in Table 3. The DIC accumulation in the hypolimnion was set to vary with the standard error of the slope of the regression line ($9.2 \pm 1.1 \text{ mg C m}^{-2} \text{ d}^{-1}$, see Results), the variation of which affects the sediment respiration rate used for all sediments (see Results and Discussion). Photooxidation was allowed to vary using the standard error of the slope ($\pm 0.6 \mu\text{g C L}^{-1} \text{ h}^{-1}$) in the regression between DOC and photooxidation rates. The mean represents what is here referred to as the "most likely mineralization." The extremes represent situations with "maximum" (high ingestion rates, low G.E., high exudate ratio, high photooxidation, and high DIC accumulation) and "minimum" (low ingestion rates, high G.E., low exudate ratio, low photooxidation, and low DIC accumulation) mineralizations, respectively. To obtain reasonable "extremes," the values for each variable (ingestion rate, G.E., etc.) were set to represent the upper and lower quartiles in the data sets used for this calculation. Higher or lower values of the different parameters may occur, but selected ranges should cover possible extremes for seasonal means.

$\delta^{13}\text{C}$ isotopic composition of DIC and POC—Stable carbon isotope analyses were used as an independent method to trace the sources of organic and inorganic carbon. POC and DIC were collected regularly as above, and surface sediment (0–2 cm) from five profundal stations along the lake. Samples were analyzed using a cryogenic purification system coupled to a Finnigan Delta S isotope ratio mass spectrometer (cf. Meili et al. 1993, 2000). Duplicate determinations usually differed by $\leq 0.1\%$.

Results

Plankton community—The plankton community biomass was dominated by bacteria (Table 2). The flagellate biomass was also high compared to the obligate autotrophic biomass. In 1995, when all ciliates were counted, the ciliate biomass was relatively large, indicating that it probably was a significant part of the total plankton biomass in 1994 also. The metazoan zooplankton biomass (mainly crustaceans) was very low. All in all, more than 80% of the total plankton biomass was heterotrophic.

Hydrology—The study period followed the spring high water flow, which was about 25 times higher than the summer mean flow. Input of water via the inlets was variable in the beginning of the study period with two small summer peaks and then leveled off to a summer minimum. The stratification depth in the epilimnion decreased from about 10 m to a minimum of about 5 m during late July, and then again increased to about 10 m. As a consequence, the epilimnion water residence time increased from about 20 d in early June to about 500 d at the end of the study period.

Carbon mass balance—The mass balance for organic carbon during the study period showed that the supply was dominated by the allochthonous input via the inlets even during the low-flow period following snow melt, while the autochthonous input from pelagic primary production was small (about 4% of TOC input, Table 4). There was a net loss of both DOC and POC from the lake water during the study period (TOC loss about 11%). Part of this loss was explained by a lake water level decrease of 0.4 m over the study period (more water flowed out of the lake than into the lake), which thereby contributed to the net loss of DOC via the outlet of the lake. The remaining apparent loss of POC (21 g C m^{-2}) agreed well with the measured sedimentation of organic carbon (18 g C m^{-2}).

Isotopic composition of POC—The $\delta^{13}\text{C}$ of POC in hypolimnetic water varied between -26.3% and -27.2% throughout the study period (Fig. 1A). This is similar to allochthonous carbon supplied from boreal forests (-27% , e.g., Meili et al. 1993). Sediment POC had slightly lower values ($-28.3\% \pm 0.1\%$, 95% confidence interval, $n = 5$). Epilimnetic POC was isotopically more variable. When primary production was low (March to June), the $\delta^{13}\text{C}$ of epilimnetic POC was $-27.6\% \pm 0.3\%$ (95% confidence interval, $n = 4$) and very similar to that of hypolimnetic POC. However, despite the overwhelming dominance of allochthonous POC (Table 4), epilimnetic POC was clearly affected by autochthonous carbon input during the summer phytoplankton maximum (Fig. 1A), showing a gradual depletion of $\delta^{13}\text{C}$ to almost -31% , whereas hypolimnetic values remained virtually unchanged (Fig. 1A).

DIC and DO balances—The accumulation of DIC and the depletion of DO in the hypolimnion after onset of stratification were linear over time (p values of the regressions

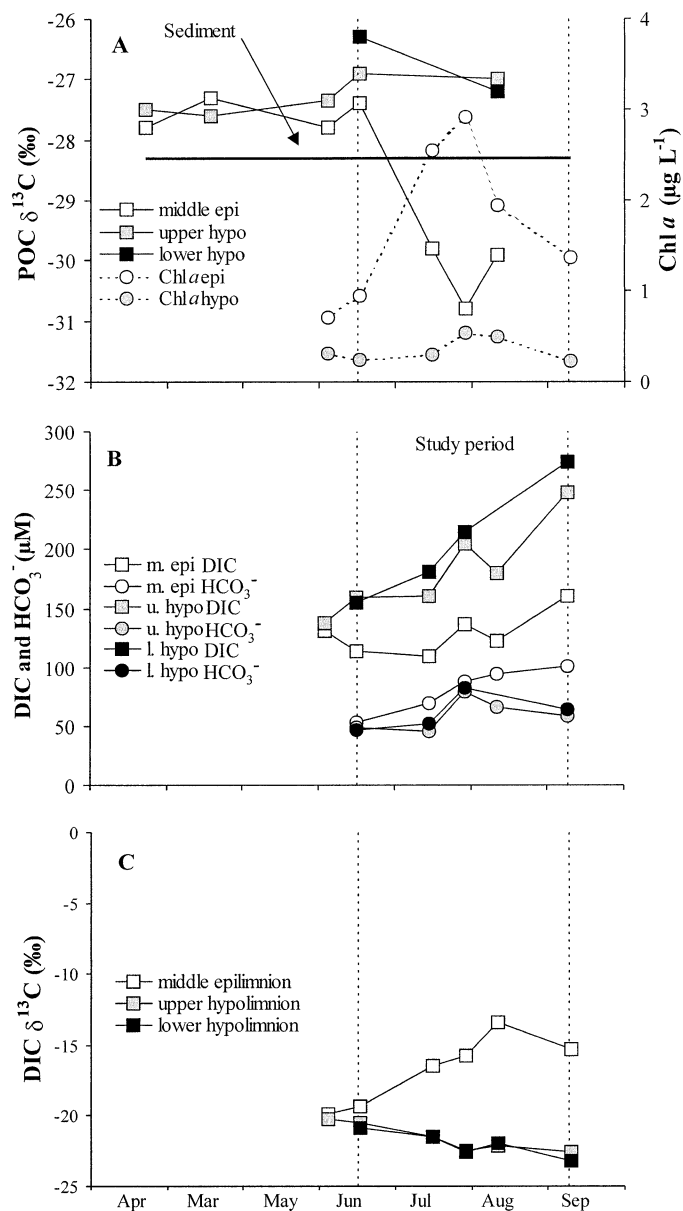


Fig. 1. (A) Isotopic composition of POC ($\delta^{13}\text{C}$), between 22 March and 10 August 1994, and the chlorophyll *a* concentration, between 3 June and 8 September 1994. (B) Concentration of DIC and HCO_3^- , and (C) isotopic composition of DIC ($\delta^{13}\text{C}$) in the middle of epilimnion and lower and upper hypolimnion. The investigation period is indicated with vertical dotted lines.

were 0.002 and 0.003, respectively) and the slopes were not significantly different (*t*-test, $p = 0.73$). Accordingly, the total summer production of DIC and the consumption of DO in the hypolimnion were similar, which suggests that production of DIC was largely due to respiration. These two independent methods indicated a total hypolimnetic mineralization of $9.2 \pm 1.1 \text{ g C m}^{-2}$ when normalized to the lake surface area. Groundwater or other inputs of DIC would have resulted in different slopes of the regression lines above and are unlikely to be significant in the geological setting of Lake Ötrasket considering the carbonate-poor bedrock dom-

inated by granites (Ivarsson and Jansson 1995), in particular since the groundwater input during the study period was only about 2% of the hypolimnion volume, if assuming a groundwater flow of around 0.5 cm d^{-1} (e.g., Cole and Pace 1998) across the hypolimnion sediment surface.

Calculations based on pH, temperature, and DIC (Stumm and Morgan 1996; Maberly 1996) suggest that the CO_2 build up in the hypolimnion during the study period (average concentration $127 \mu\text{M}$ or $2,300 \mu\text{atm}$) was 5–10 times above the atmospheric equilibrium ($360 \mu\text{atm}$, measured by the lake in summer 2000, Aronsen unpubl. data). In the epilimnion water, such calculations indicated a threefold supersaturation (range 1.9–3.4 times) of CO_2 relative to the atmospheric equilibrium during the whole summer season (average concentration $45 \mu\text{M}$ or $1,050 \mu\text{atm}$), which is typical for summer surface waters in Swedish forest lakes (Meili, unpubl. data, compiled by Cole et al. 1994). The values above are supported by direct measurements of the partial pressure of CO_2 in surface water ($1,200\text{--}1,600 \mu\text{atm}$) and hypolimnion water ($2,300 \mu\text{atm}$) from Lake Ötrasket in the summer 2000, which was a year with higher DOC concentrations (Aronsen unpubl. data). At the end of the study period, about 60% of DIC in epilimnion water consisted of HCO_3^- , while in the hypolimnion DIC was dominated by CO_2 (Fig. 1B).

Isotopic composition of DIC—During spring overturn, DIC had a uniform isotopic composition throughout the water column (Fig. 1C). The highly negative $\delta^{13}\text{C}$ value of -20‰ indicated a predominance of respiratory CO_2 from decomposition of organic matter from terrestrial production ($\delta^{13}\text{C} = -27\text{‰}$) over geogenic DIC sources such as limestone weathering ($\delta^{13}\text{C} = -0\text{‰}$), a feature shared with other boreal softwater lakes (e.g., Meili et al. 1993). During summer stratification, values in the hypolimnion declined gradually to about -23‰ , and upper and lower strata always showed practically identical values (Fig. 1C). In contrast, the $\delta^{13}\text{C}$ of DIC in the epilimnion gradually increased to reach levels fluctuating around -13 to -17‰ , suggesting a partial exchange with atmospheric CO_2 ($\delta^{13}\text{C} = -8\text{‰}$) and/or a different relative contribution of groundwater in the inflowing water (see Discussion).

Mineralization of organic carbon in the lake—The divergence of the $\delta^{13}\text{C}$ values of DIC in the epilimnion and the hypolimnion after onset of stratification (Fig. 1C), the linearity of the hypolimnetic change in $\delta^{13}\text{C}$ and [DIC], and the similarity of $\delta^{13}\text{C}$ values in both the upper and the lower hypolimnion (Fig. 1C) all suggest that the hypolimnion can be considered as a sealed volume separated from surficial water layers and the atmosphere. Changes over time in dissolved concentrations (Fig. 1B) can thus be interpreted as the result of processes in a closed reactor. This enabled us to calculate the total mineralization of organic carbon in the hypolimnion and contributions from different compartments to this mineralization (Table 5). The contribution of DIC from hypolimnetic sediment respiration was calculated by subtracting the pelagic community respiration in the hypolimnion (3.1 g C m^{-2} , Table 5) from the observed accumulation of DIC ($9.2 \pm 1.1 \text{ g C m}^{-2}$) and was found to account

Table 5. Partitioning of organic carbon mineralization (g C m^{-2}) in different lake strata during summer stratification 1994 (84 d). The range column shows minimum and maximum estimates of respiration in the whole lake calculated from the upper and lower extremes shown in Table 3 (see Methods). Total mineralization represents the sum of pelagic heterotrophic (bacteria + flagellates + ciliates + metazoans) respiration, photooxidation, and sediment respiration. All estimates are normalized to the lake surface area.

	Epilimnion	Metalimnion	Hypolimnion	Whole lake	Range
Pelagic heterotrophs	6.1	4.4	3.1	13.6	9.2–20.7
Bacteria	4.1	3.1	2.2	9.4	6.5–14.7
Flagellates	1.2	0.9	0.6	2.7	1.7–4.1
Ciliates	0.6	0.3	0.2	1.1	0.7–1.6
Metazoans	0.2	0.1	0.1	0.4	0.3–0.3
Photooxidation	2.0	0	0	2.0	1.7–2.3
Sediment respiration	2.3	2.7	6.1	11.1	10.8–10.3
Total mineralization	10.4	7.1	9.2	26.7	21.7–33.3

for about 65% of the total mineralization in the hypolimnion (Table 5). The hypolimnetic sediment mineralization rate could thus be estimated to about $132 \text{ mg C m}^{-2} \text{ d}^{-1}$.

Bacterial production and respiration in epilimnion water culminated in early July, clearly before the peak in net primary production (NPP) that occurred in August (Figs. 2A and 2B). Mineralization in epilimnion water was dominated by respiration of bacteria and flagellates. Photooxidation of organic carbon was significant, contributing almost 20% of the total epilimnetic mineralization. About 20% of the epilimnetic mineralization was estimated to occur in the sediments (Table 5).

Whole-lake mineralization of organic carbon was estimated to be about 27 g C m^{-2} (range $22\text{--}33 \text{ g C m}^{-2}$, Table

5) during the investigation period. About 40% (range 30–50%) was mineralized in sediments, about 10% by photooxidation, and 50% (range 40–60%) by biotic respiration in the pelagial. Bacterial mineralization was clearly most important in the pelagial, contributing about 60% of the total pelagic mineralization, followed by protozoan and metazoan zooplankton (30%) and photooxidation (10%). The relative importance of different organism groups changes little when considering the possible errors introduced by uncertainties of different assumptions (Table 3, Table 5).

Contribution from different pools of organic matter to mineralization—Table 6 presents the contribution from different organic carbon pools to mineralization. Of the pelagic organic carbon pool, only about 2% (about 5 g C m^{-2}) was estimated to originate from photosynthetic activity, whereas the rest (about 230 g C m^{-2}) was fluvial input of allochthonous organic matter from terrestrial parts of the watershed. Autochthonous organic carbon could at most have contributed about 20% of the mineralization of organic carbon in the whole lake, and about half of the epilimnetic mineralization. Pelagic turnover of allochthonous organic carbon was highest in the metalimnion, but this may be influenced by the assumption that all autochthonous production was mineralized in epilimnetic water (Table 6). Turnover of organic carbon in the sediment (mostly POC) was much higher (Table 6) than in the pelagial (mostly DOC).

Allochthonous versus autochthonous carbon as a source of mineralization—The maximum contribution of autochthonous carbon to carbon mineralization during different seasons was estimated by assuming that 100% of primary production was mineralized between sampling events. The maximum relative contribution of autochthonous carbon could thereby be calculated by dividing primary production with total mineralization. Results (Fig. 3) showed that autochthonous carbon was an important potential source to mineralization during the phytoplankton maximum in August, but not otherwise, and stresses the large importance of allochthonous carbon even during the summer season.

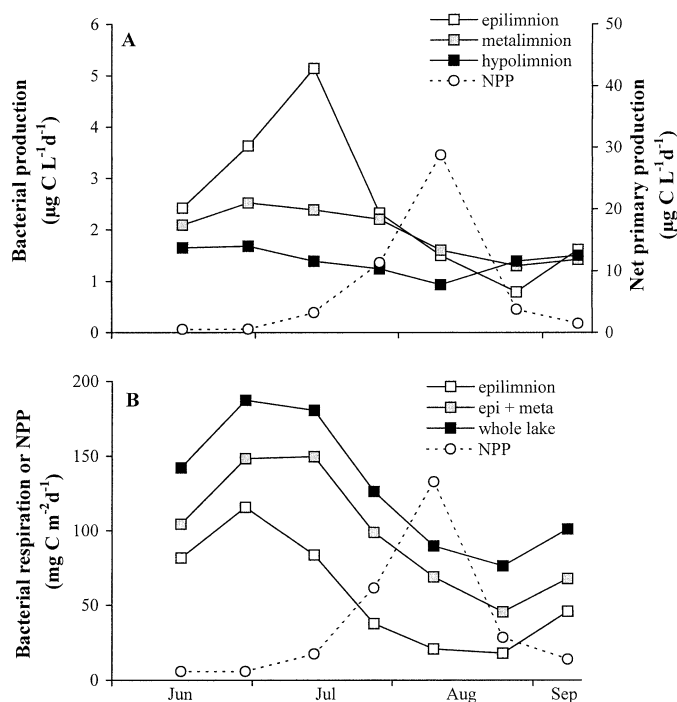


Fig. 2. (A) Pelagic bacterial net production in different strata and estimated net primary production (NPP) in epilimnion (June 16–September 8 1994). (B) Pelagic bacterial respiration in different strata and estimated NPP in the epilimnion. Values are normalized to the lake surface area.

Discussion

The ensemble of available data allows for an unusually detailed assessment of the sources and sinks of organic car-

Table 6. Turnover of the allochthonous carbon pool and the autochthonous season production of organic carbon (DOC + POC). Epilimnion, metalimnion, and hypolimnion represent the pelagial only. The sediment pool of allochthonous organic carbon represents gross sedimentation of organic carbon during 1 yr (Jonsson and Jansson 1997). All estimates are normalized to the lake surface area.

	Pool or production		Total carbon mineralization (g C m ⁻²)	Turnover	
	Allochthonous carbon (g C m ⁻²)	Autochthonous carbon (g C m ⁻²)		Allochthonous carbon (%)	Autochthonous carbon (%)
Epilimnion	105	4.7	8.1	≈3	≈100
Metalimnion	45	≈0	4.4	≈10	≈100
Hypolimnion	81	0	3.1	4	—
Sediment	54	0	11.1	21	—
Total	285	≈5	27	≈9	≈100

bon in a humic lake during a summer season. The cycling of organic carbon also controls the cycling of inorganic carbon, which accounts for only a minor fraction of the total carbon pool in the water. The sum of all individual mineralization processes of organic carbon in Lake Örtträsket during the summer of 1994 amounted to a total of about 27 g C m⁻² or 0.3 g C m⁻² d⁻¹ (Table 5), which was calculated using several independent methods. Loss of TOC in the mass balance for the lake water (11 g C m⁻², Table 4) was approximately 75% of the estimated pelagic mineralization from heterotrophic organisms and photooxidation, with a range of 48–101% depending on the possible uncertainties introduced by different assumptions (Table 5). The good agreement between these independent methods for estimating organic carbon mineralization indicates that our estimates are reasonably accurate.

Most of the carbon mineralized was not recycled but lost from the system. While part of the mineralization is manifested in a temporary net accumulation of DIC in the hypolimnion (Fig. 1B, Table 5), most of the mineralization (18 g C m⁻²) occurred in the upper strata of the lake, where most of the CO₂ produced probably was lost to the atmosphere (in the lake or immediately downstream). This assumption is supported by the difference in CO₂ concentration between epilimnion and hypolimnion, and its magnitude

agrees very well with the expected CO₂ evasion from the lake (16 g C m⁻²), estimated from the CO₂ supersaturation in the epilimnion (about threefold atmospheric equilibrium, mean excess CO₂ of 31 μM) and a commonly used lake-atmosphere transfer coefficient (piston velocity) of 0.5 m d⁻¹ (e.g., Cole et al. 1994).

The role of primary production in carbon mineralization can be elucidated by comparison with the total loss of organic carbon. It is evident that autochthonous carbon could have contributed only 30–40% of the total mineralization in the water, or about 20% of total lake mineralization (Tables 4 and 5), even during a summer with high production and low water flow. The importance of autochthonous carbon was greatest in the epilimnion where it at most (depending on the degree of use) could have supported about half of the carbon mineralization during the study period, and primary production may have been a dominant source for mineralization in the lake only during the phytoplankton maximum in August (Fig. 3). Part of POC and DOC from primary producers must have been lost from the lake through the outlet. However, this loss was probably small since the epilimnion water residence time had become longer during the primary production peak (about 100 d). Part of the primary-produced organic carbon may also have been permanently withdrawn by sedimentation, but this fraction was probably small as well (*see below*). These comparisons strongly suggest that allochthonous organic carbon was the principal source for mineralization in the lake as a whole.

Direct evidence for the dominance of allochthonous input in the supply of organic carbon to mineralization is given by stable isotope data. At the start of summer stratification, the highly depleted δ¹³C of DIC in the epilimnion was identical to that in the hypolimnion (Fig. 1A) and shows that mineralized organic carbon was the major source of DIC in the whole lake at that time. This was probably to a large extent caused by a large input of “high” quality allochthonous DOM with the spring flood that is used by bacteria (Bergström and Jansson 2000). The low level of the δ¹³C of DIC in the lake and its gradual decrease in the hypolimnion (Fig. 1C) are evidence of a continuous input of CO₂ from mineralization of organic carbon, also during summer. The observed δ¹³C trend is quantitatively consistent with the simultaneous increase in DIC concentration (Fig. 1B) if a δ¹³C of -27‰ in the source material is assumed, clearly suggesting an organic matter source that has an isotopic sig-

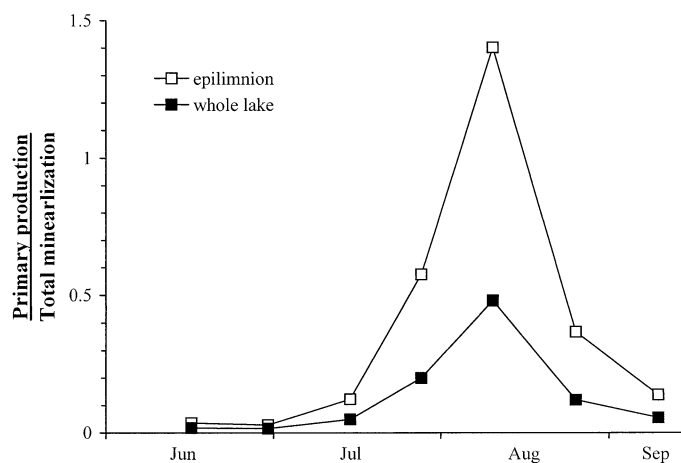


Fig. 3. Seasonal variation in the ratio between autochthonous produced carbon (DOC + POC) and the total carbon mineralization in the lake during the study period.

nature similar to allochthonous organic matter, hypolimnion POM, and surface sediment, rather than autochthonous organic matter (see below). The contribution of methane oxidation to the observed DIC accumulation in the hypolimnion has been assumed negligible and can be excluded since it would have generated a much lower $\delta^{13}\text{C}$ value of DIC (cf. Conway et al. 1994) and resulted in inconsistencies in the isotopic mass balance, and also considering the high concentration of DO in the bottom water ($>6 \text{ mg L}^{-1}$). In contrast to the hypolimnion, the $\delta^{13}\text{C}$ of POC in the epilimnion showed a considerable depletion during the phytoplankton maximum (Fig. 1A) consistent with an autochthonous organic matter input to the POM pool. Purely primary-produced POC in Lake Örräsket had $\delta^{13}\text{C}$ values $< -35\%$, possibly $< -40\%$, during the study period, based on zooplankton $\delta^{13}\text{C}$ analyses (Meili et al. 2000). Such low values are required to obtain a measurable influence on the isotopic composition of bulk POC that on average consisted to $>90\%$ of detrital POC (Table 2) of most likely allochthonous origin, and are also consistent with the dominance of respiratory DIC with a highly negative $\delta^{13}\text{C}$ serving as substrate for primary production (cf. Meili et al. 1993; Jones et al. 1999; Meili et al. 2000). The DIC in the epilimnion showed after spring turnover an enrichment with DIC from a different source than in hypolimnion. This may be partly due to physical exchange of dissolved CO_2 with atmospheric CO_2 ($\delta^{13}\text{C} = -8\%$). Another explanation supported by the simultaneous increase in the concentration of HCO_3^- in the epilimnion (Fig. 1B) is a higher share of groundwater, with a less negative $\delta^{13}\text{C}$ value, in the inlet water than during spring runoff. In this case, the $\delta^{13}\text{C}$ of CO_2 is more negative than indicated by the $\delta^{13}\text{C}$ of DIC (Mook et al. 1974), which again supports respiration as a major source of dissolved CO_2 . The fact that both the concentration and the isotopic composition of DIC in the epilimnion remained at levels far from equilibrium with the atmosphere throughout the summer is evidence for a continuous mineralization in excess of primary production. Stable isotope data thus indicate that most of the DIC in the lake to a dominant share was supplied by mineralization of organic carbon resulting in a highly depleted signature of primary produced POM. This material is quantitatively insignificant to affect the mineralization (and thus DIC signature) in the hypolimnion. Possibly, a fraction of the primary-produced organic carbon may have been permanently withdrawn by sedimentation, as indicated by the sediment isotopic composition (Fig. 1A).

Most of the mineralization of organic carbon in the water column was due to bacterial respiration (Table 5). The contribution from other planktonic heterotrophs was only about half of that from bacterioplankton. It is worth noting that the combined respiration of flagellates, ciliates, and metazoan zooplankton approximately equaled the sum of net production by bacterioplankton and phytoplankton, which is reasonable since these organisms are the major consumers of bacterioplankton and phytoplankton in Lake Örräsket. Next to bacteria, flagellates contributed most to mineralization, which is in line with their role as the dominant consumers of bacterioplankton in the lake (Jansson et al. 1999). Assuming that all net production by flagellates and ciliates was consumed (see *Methods*) may overestimate plankton respi-

ration, but for the purpose of this study the potential error is unlikely to be of significance (see Table 5).

Photooxidation was, according to our estimates, of little importance for the whole-lake carbon mineralization, an expected result for a large, deep humic lake like Lake Örräsket. Nevertheless, if only the epilimnion is considered, the DIC production from photooxidation accounted for approximately 20% of the total mineralization, in spite of the fact that photooxidation took place only in the uppermost layer of the 5–15 m deep epilimnion. We may even have underestimated photooxidation because the PAR (but not UVA) radiation applied in the experiment was comparatively low (Bertilsson et al. 1999), but this is unlikely since UVA radiation is far more important in the photomineralization of DOC in humic lakes (Vähätalo et al. 2000). Further, it has been demonstrated by recent studies in humic lakes (Bertilsson et al. 1999) that light can generate low molecular weight organic molecules that are highly valuable as bacterial substrate. If such a photomodification of DOC stimulated bacterial respiration in Lake Örräsket, the total effect of light on mineralization might have been greater than indicated here, although without influencing the flux estimates. Our estimate of the importance of photooxidation for the whole-lake mineralization of organic matter is comparable to studies of the water column from smaller and from more shallow lakes, also with different DOC contents (Granéli et al. 1996; Reitner et al. 1997), possibly indicating that rates of other mineralization processes change correspondingly with the photooxidation.

A large share of the whole-lake mineralization took place in the sediments (about 40%, range 30–50%, Table 5). Our estimate of sediment respiration was based on the measurements in the hypolimnion, which were assumed to be relevant also for sediments in the epilimnion and the metalimnion. This introduces uncertainties since differences in temperature (Bell and Ahlgren 1987), abundance of organic carbon (Sander and Kalff 1993), and quality of organic carbon (Sinsabaugh and Findlay 1995) between shallow and deep sediments can affect the mineralization rate. We may have underestimated mineralization in epilimnetic sediments by not accounting for the temperature difference between epilimnion and hypolimnion (Table 1). However, it is more likely that we overestimated the sediment mineralization by assuming the same mineralization rates in all sediments because of differences in abundance of substrates. Other studies in Lake Örräsket have shown that the supply and content of organic carbon is higher in hypolimnetic sediments than in sediments of the metalimnion and the epilimnion, which can be characterized as erosion and transport bottoms (Malmgren and Jansson 1995; Jonsson and Jansson 1997). Nevertheless, it is obvious that even in lakes where input of organic carbon is totally dominated by allochthonous carbon in dissolved form, the role of sediments cannot be neglected when evaluating the role of different metabolic processes on organic carbon cycling.

An aspect of principal interest is the relationship between pelagic and benthic mineralization. In the deep Lake Örräsket, the contribution of sediment mineralization was relatively large (Table 5). Apparently, this was largely related to the much higher turnover of sediment carbon (mainly POC)

than lake water carbon (mainly DOC), 21% compared to 3–10%, respectively (Table 6). In a previous paper (Jonsson and Jansson 1997), it was shown that POM supplied by high discharge events, mainly during spring flood in May, rapidly settled out of the water column and formed the major substrate for sediment respiration during summer in Lake Öträsket. The difference in degradability between sediment POM and lake water DOM may have been a result of the different origin and composition of these pools. Settling POM was apparently less degraded, as indicated by a C:N mass ratio of 15:1, (Jonsson and Jansson 1997) than the DOM flowing into the lake (C:N mass ratio of about 25:1, Jonsson 1997). Another factor that may contribute to high mineralization rates in the sediments is that the availability of inorganic nutrients is higher in the sediment than in the lake water. Previous experiments have demonstrated that bacterial activity in the water column can be considerably enhanced by increasing the supply of inorganic nutrients (Jansson et al. 1999), which suggests that the mineralization rate in the water column may be slowed down by inorganic nutrient limitation. Our results indicate that the sediment may well dominate the total carbon mineralization in many boreal lakes, which typically are more shallow than Lake Öträsket.

This study has demonstrated that carbon mineralization during summer stratification in Lake Öträsket had three principal sources: (1) Allochthonous POM entering predominantly during high flow in spring, (2) allochthonous DOM supplied continuously, and (3) fresh autochthonous organic carbon produced in the epilimnion during the summer. Of these sources, the large amounts of terrestrial carbon introduced in dissolved and particulate forms was virtually always more important for the total CO₂ production than organic carbon produced in the lake, even though the availability to degradation may be far higher for autochthonous carbon.

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Received: 7 November 2000

Accepted: 24 July 2001

Amended: 24 July 2001