



Fluxes of methane, carbon dioxide and nitrous oxide in boreal lakes and potential anthropogenic effects on the aquatic greenhouse gas emissions

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Abstract

We have examined how some major catchment disturbances may affect the aquatic greenhouse gas fluxes in the boreal zone, using gas flux data from studies made in 1994–1999 in the pelagic regions of seven lakes and two reservoirs in Finland. The highest pelagic seasonal average methane (CH₄) emissions were up to 12 mmol m⁻² d⁻¹ from eutrophied lakes with agricultural catchments. Nutrient loading increases autochthonous primary production in lakes, promoting oxygen consumption and anaerobic decomposition in the sediments and this can lead to increased CH₄ release from lakes to the atmosphere. The carbon dioxide (CO₂) fluxes were higher from reservoirs and lakes whose catchment areas were rich in peatlands or managed forests, and from eutrophied lakes in comparison to oligotrophic and mesotrophic sites. However, all these sites were net sources of CO₂ to the atmosphere. The pelagic CH₄ emissions were generally lower than those from the littoral zone. The fluxes of nitrous oxide (N₂O) were negligible in the pelagic regions, apparently due to low nitrate inputs and/or low nitrification activity. However, the littoral zone, acting as a buffer for leached nitrogen, did release N₂O. Anthropogenic disturbances of boreal lakes, such as increasing eutrophication, can change the aquatic greenhouse gas balance, but also the gas exchange in the littoral zone should be included in any assessment of the overall effect. It seems that autochthonous and allochthonous carbon sources, which contribute to the CH₄ and CO₂ production in lakes, also have importance in the greenhouse gas emissions from reservoirs.

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1. Introduction

Forests and wetlands in the boreal zone contain large amounts of organic matter in vegetation and soils (Ka-

uppi et al., 1997). This emphasizes their role in the global carbon (C) and nitrogen (N) cycles, including the atmospheric budgets of radiatively important greenhouse gases CH₄, CO₂ and N₂O. Numerous studies have assessed the greenhouse gas balances in boreal terrestrial ecosystems, such as peatlands (e.g., Nykänen et al., 1998), whereas aquatic ecosystems in these landscapes have generally been neglected. However, because there are a large number of lakes in the boreal zone, data on their greenhouse gas exchange would improve our

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understanding of the fundamentals of boreal regional greenhouse gas budgets. The CO₂ and CH₄ emissions from the world's freshwater reservoirs have recently been estimated to be equivalent to 4% and 18% of other anthropogenic CO₂ and CH₄ emissions, respectively (St. Louis et al., 2000). However, to obtain a better estimate of the atmospheric importance of natural lakes, more data are needed from lakes situated in different geographical regions.

Biogeochemical processes in lakes are closely linked to their immediate terrestrial ecosystems because lakes receive allochthonous C and nutrients from their catchment areas via streams and through groundwater and surface water inflow. For example, in the boreal zone, the organic C content in lake water depends on the abundance of wetlands and forests in the catchment (Hope et al., 1996). A part of the terrigenous organic C entering lakes from the catchment is respired as CO₂ to the atmosphere. Due to the large supplies of allochthonous organic C, northern lakes can be 'net heterotrophic', i.e. the respiration in the lakes exceeds phytoplankton primary production (Cole, 1999; Cole et al., 2000). The lake CO₂ saturation can additionally be enhanced by inputs of dissolved inorganic C (e.g., Striegl and Michmerhuizen, 1998). Cole et al. (1994) demonstrated that of the samples collected from lakes situated around the world, most were supersaturated with CO₂ with respect to the atmospheric equilibrium. Therefore, the world's lakes appear to predominantly release CO₂ to the atmosphere. Due to the close linkage between lakes and their catchments, it is obvious that catchment disturbances, such as land-use changes, can disrupt the lake greenhouse gas balances.

In boreal rural regions, agriculture and forestry are important sources of the nutrients entering lakes, with nitrogen and phosphorus (P) being the most important elements (Cooke and Prepas, 1998). Increased nutrient input into lakes causes eutrophication (Carpenter et al., 1998). The increased availability of easily degradable autochthonous organic matter increases decomposition and oxygen consumption, promoting oxygen depletion in the water column and sediment. Anoxic conditions can increase CH₄ emissions from lakes by enhancing the CH₄ production and/or decreasing the CH₄ oxidation (Kiene, 1991) and low oxygen availability can also promote N₂O production. Nitrous oxide generation in lakes generally requires steep oxygen gradients allowing sequential aerobic nitrification and anaerobic denitrification to take place (Seitzinger, 1990). High emissions of CH₄ (Casper et al., 2000) and increased concentrations of N₂O (Mengis et al., 1997) have been measured from the water columns of nutrient enriched temperate lakes. This implies that eutrophied boreal lakes could also be supersaturated with CH₄ and N₂O and act as sources of these gases to the atmosphere. Lakes with high primary production can have an influx of CO₂ from the atmo-

sphere due to increased photosynthesis (Schindler et al., 1972; Cole et al., 2000).

We summarize here the results from studies on the greenhouse gas fluxes from Finnish lakes and reservoirs, and show how some major catchment disturbances that affect the lake water quality may induce changes in the greenhouse gas emissions from boreal lakes. The CH₄ and CO₂ fluxes are compared with those previously reported from other temperate and boreal ecosystems to provide an overview of the potential importance of aquatic greenhouse gas emissions in boreal regions.

2. Case studies in Finnish lakes and reservoirs

2.1. Study sites

The fluxes of CH₄, CO₂ and N₂O have been studied in years 1994–1999 in the pelagic regions of seven lakes and two hydroelectric reservoirs in the boreal zone in Finland (Fig. 1). The lakes in Finland are post-glacial (Saarnisto, 2000). The bedrock in Finland is mostly Precambrian covered by quaternary deposits. Most of

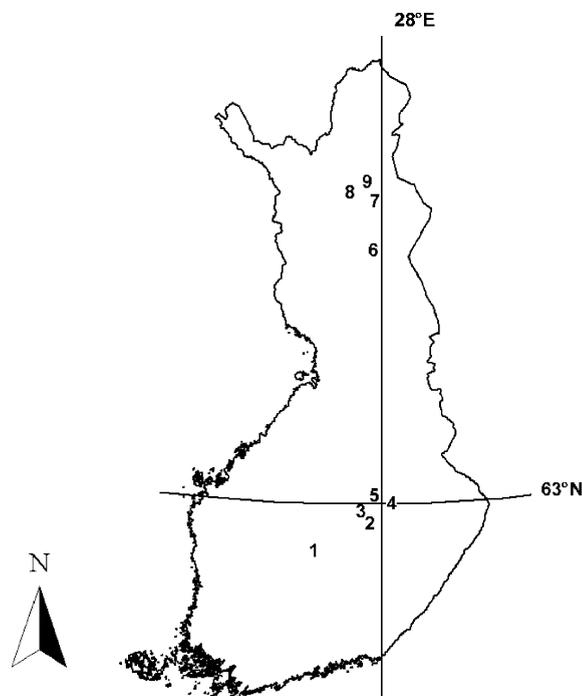


Fig. 1. Locations of the boreal Finnish ponds, lakes and reservoirs where the greenhouse gas fluxes have been studied during the period 1994–1999. The sites are: (1) Lake Heinälampi, (2) Lake Vehmasjärvi, (3) Lake Mäkijärvi, (4) Lake Postilampi, (5) Lake Kevätön, (6) Jänkääläisenlampi Pond, (7) Reservoir Lokka, (8) Reservoir Porttipahta and (9) Kotsamolampi Pond.

the C in Finnish lakes is of biogenic origin (Pajunen, 2000). Finnish lakes are generally brown due to the presence of humic substances and relatively rich in total P. Only 3% of Finnish lakes are considered to be N limited (Mannio et al., 2000). About 9% of the lakes in the country are clearly eutrophied, having total P concentration above $35 \mu\text{g l}^{-1}$ (Mannio et al., 2000). The lakes can thermally stratify during summer and winter ice-cover. In the transition of the southern and middle boreal zones, where five of the nine sites (sites 1–5, Fig. 1) were located, the lakes are generally ice-covered from late November to early May. The reservoirs in the northern boreal zone are ice-covered from late October to early June.

The study lakes were small varying in area from 0.01 to 4.07 km², whereas the reservoirs were among the largest in western Europe (Table 1). In Finland, the lakes with an area of 0.01–10 km² account for 99% of the total number and 34% of the total area of lakes larger than 0.01 km² (Raatikainen and Kuusisto, 1990). Both the study lakes and reservoirs were shallow, as are most lakes in Finland (Raatikainen and Kuusisto, 1990). The trophic state of the sites varied from oligotrophic to eutrophic (Table 1). Reservoirs Lokka and Porttipahta have been flooded for hydroelectric power generation since 1967 and 1970, respectively, and previous peatlands or upland forests dominate their bottoms. The catchment of humic Jänkäläisenlampi Pond (average water colour 140 mg Pt l^{-1}) is dominated by peatlands, while upland forests dominate the catchment of the

clear, acidic Kotsamolampi Pond. Lakes Postilampi, Heinälampi and Kevätön have become more eutrophic as a result of intensive agriculture in their catchments, and Lakes Heinälampi and Kevätön have also received sewage. The eutrophic Lake Vehmasjärvi had the darkest epilimnic water (colour up to 240 mg Pt l^{-1}) indicating high organic matter input from the catchment area rich in peatlands and managed forests. The oligotrophic Lake Mäkijärvi had forest clear-cutting in its catchment during the first study year. The possible effects of the cutting on the water quality could not be properly assessed because there were no appropriate long-term data on the water quality in the lake.

The 4–5 sampling stations in the reservoirs were chosen to represent various bottom types and water depths (Huttunen et al., 2002b). The station in Lake Heinälampi had a depth of 3.5 m, whereas the ponds and Lake Postilampi were sampled in the deepest pelagic zone. Lakes Kevätön, Vehmasjärvi and Mäkijärvi were the most intensively studied sites with monthly gas flux measurements from May to October in 1997 and 1998 (Huttunen et al., 1999) and with measurements of the accumulation of gases in the water column during winter in 1997–1999 (Huttunen et al., 2001a). These lakes had three sampling stations: (i) at the deepest point of the lake, (ii) in the 3–5 m deep shallow pelagic zone, and (iii) in the <2 m deep infralittoral (Huttunen et al., 1999). The two deepest stations were situated in the open water area, whereas the infralittoral stations were dominated by *Nuphar lutea* (L.) Sibth. and Sm. In Lakes Postilampi

Table 1
Summary of the characteristics of the reservoirs, ponds and lakes in the Finnish greenhouse gas flux studies

Site	Year ^a	Area (km ²)	Mean depth (m)	Max. depth (m)	Trophic state ^b	Bottom/catchment characteristics ^c
Reservoir Lokka	1994–95	417 ^d	5.0 ^d	10.0 ^d	Eutrophic	Peatland 76%, upland forest 21%
Reservoir Porttipahta	1995	214 ^d	6.3 ^d	34.5 ^d	Mesotrophic	Peatland 45%, upland forest 55%
Jänkäläisenlampi Pond	1994	0.01	ND ^c	1.8	Mesotrophic	Peatland 95%, upland forest 5%
Kotsamolampi Pond	1995	0.01	ND	3.2	Mesotrophic	Peatland 20%, upland forest 80%
Lake Postilampi	1996–98	0.03	3.2	4.3	Eutrophic	Peatland 0%, upland forest 60%, agricultural land 31%
Lake Heinälampi	1996	0.098	ND	5.0	Eutrophic	Peatland 6%, upland forest 63%, agricultural land 23%
Lake Kevätön	1997–99	4.07	2.3	10.1	Eutrophic	Peatland 3%, upland forest 35%, agricultural land 30%
Lake Vehmasjärvi	1997–99	0.41	3.9	18.7	Eutrophic	Peatland 25%, upland forest 61%, agricultural land 3%
Lake Mäkijärvi	1997–99	0.20	3.4	8.7	Oligotrophic	Peatland 5%, upland forest 73%, agricultural land 0%

^a Year of the greenhouse gas flux studies.

^b Classified based on average summertime total phosphorus or chlorophyll *a* concentrations in the epilimnion according to Forsberg and Ryding (1980).

^c Bottom characteristics are given for reservoirs, and catchment characteristics for ponds and lakes. Peatlands consist about 30% of the catchments of the reservoirs.

^d Maximum values in the regulated reservoirs.

^e Not determined.

and Kevätön, greenhouse gas fluxes have been measured in the littoral zone and other lake-associated wetlands (Huttunen et al., 2000; Juutinen et al., 2003). The cycling of greenhouse gases and nutrients has been studied in the sediment cores of Lake Kevätön, and CH₄ oxidation in its water column has been determined (Liikanen, 2002).

2.2. Gas flux measurements

The fluxes of CH₄, CO₂ and N₂O across the water–air interface were measured during the open water season with floating static chambers (Huttunen et al., 2002a,b), usually with two aluminum and one transparent chambers. In the reservoirs and ponds, only aluminum chambers were used for the measurement of the CO₂ flux, which may cause some overestimation of the actual CO₂ release resulting from the disturbances in the photosynthetic CO₂ uptake in the surface water. For the other lakes, a transparent chamber was used in the CO₂ exchange studies. Submerged funnel gas collectors were used for the monitoring of CH₄ ebullition (Huttunen et al., 2001b) during the summer at all of the stations. Ebullition did not contribute significantly to the CO₂ and N₂O emissions (Huttunen et al., 2001b, 2002b).

The water column in Lakes Kevätön, Vehmasjärvi, Mäkijärvi and Postilampi was sampled during late winter stratification for dissolved greenhouse gas concentrations. The accumulation of gases in the water

column was then calculated allowing us to make an estimation of potential CH₄, CO₂ and N₂O emissions at spring ice melt (Huttunen et al., 2001a, 2003; also see Striegl and Michmerhuizen, 1998). Ebullition was studied in Lake Postilampi in winter (Huttunen et al., 2003).

3. Greenhouse gas fluxes in Finnish lakes and reservoirs

3.1. Greenhouse gas fluxes during open water season

The seasonal mean CH₄ fluxes varied greatly among the Finnish study sites, and between the years, but all sites were sources of CH₄ to the atmosphere during the open water season (Table 2). There are results that the CH₄ production in freshwater sediments increases with increasing lake trophy (Casper, 1992), and furthermore the CH₄ production is dependent on the input of fresh organic matter to the sediment (Kelly and Chynoweth, 1981). Methane oxidation in the aerobic surface sediment can consume over 90% of the CH₄ produced (Kiene, 1991). High rates of CH₄ oxidation are also possible in the stratifying water columns present in northern lakes (Kiene, 1991; Liikanen, 2002). Therefore, CH₄ oxidation can effectively reduce the diffusive flux of CH₄ from lakes to the atmosphere. In the Finnish data (Table 2), highly eutrophic Lakes Postilampi and Kevätön in the agricultural catchments had the highest mean CH₄

Table 2
Mean CH₄ and CO₂ fluxes to the atmosphere from some Finnish reservoirs, ponds and lakes during the open water season

Site	Year	Stations	CH ₄ (mmol m ⁻² d ⁻¹)		CO ₂ (mmol m ⁻² d ⁻¹)		Reference
			Mean ^a	Range	Mean ^a	Range	
			Reservoir Lokka	1994	5	0.77	
	1995	5	2.1	0.33–7.4 ^b	45	20–73	Huttunen et al. (2002b)
Reservoir Porttipahta	1995	4	0.22	0.16–0.30	35	20–52	Huttunen et al. (2002b)
Jänkäläisenlampi Pond	1994	1	0.47		12		Huttunen et al. (2002a)
Kotsamolampi Pond	1995	1	0.22		0.38		Huttunen et al. (2002a)
Lake Postilampi	1996	1	3.6		6.6		Unpublished data, Huttunen et al. (2001b)
	1997	1	3.7		18		Unpublished data
	1998	1	4.9		29		Unpublished data, Huttunen et al. (2000)
Lake Heinälampi	1996	1	0.37		13		Unpublished data
Lake Kevätön	1997	3	5.1	0.98–12	14	–1.8–25	Unpublished data
	1998	3	3.2	0.28–8.3	15	9.1–19	Unpublished data, Huttunen et al. (1999)
Lake Vehmasjärvi	1997	2	0.35	0.33, 0.36	11	3.9, 19	Unpublished data
	1998	3	0.11	0.07–0.14	28	25–32	Unpublished data, Huttunen et al. (1999)
Lake Mäkijärvi	1997	2	0.18	0.15, 0.21	5.8	4.7, 6.8	Unpublished data
	1998	3	0.11	0.09–0.12	12	8.4–15	Unpublished data, Huttunen et al. (1999)

^a Mean fluxes for the sites measured by floating chambers, and the range of the mean fluxes at the different sampling stations. The potential fluxes at spring ice melt are not included in the data.

^b The CH₄ ebullition, measured with the funnel gas collectors during open water season averaged 12 and 2.9 mmol m⁻² d⁻¹ in Lokka in 1994 and 1995, respectively, and 0.05 mmol m⁻² d⁻¹ in Porttipahta in 1995 (Huttunen et al., 2002b).

emissions ($3.2\text{--}5.1\text{ mmol m}^{-2}\text{ d}^{-1}$), which were attributed to their high productivity that could support significant CH_4 production in the sediments (Huttunen et al., 1999, 2000, 2001b; also see Liikainen, 2002). In Lake Kevätön, for example, the CH_4 flux to the atmosphere increases during the summer with increasing water temperature and the development of oxygen deficiency near the sediment (Fig. 2). According to microcosm experiments in the laboratory, temperature and oxygen availability are the important factors controlling the CH_4 release from the sediments of Lake Kevätön (Liikainen, 2002).

In spite of the high CH_4 oxidation in the water column of the lake during the short summer stratification (Liikainen, 2002), the CH_4 emissions to the atmosphere were generally high. In Lakes Kevätön and Postilampi, ebullition played an important role in the total CH_4 emissions (see Fig. 3) (Huttunen et al., 1999, 2000, 2001b). Bubbling is an important mechanism for CH_4 to escape from organic-rich, methanogenic sediments through the water column to the atmosphere, and the ebullition rate is closely tied to the production of CH_4 (Kiene, 1991). When CH_4 is released from the sediments by

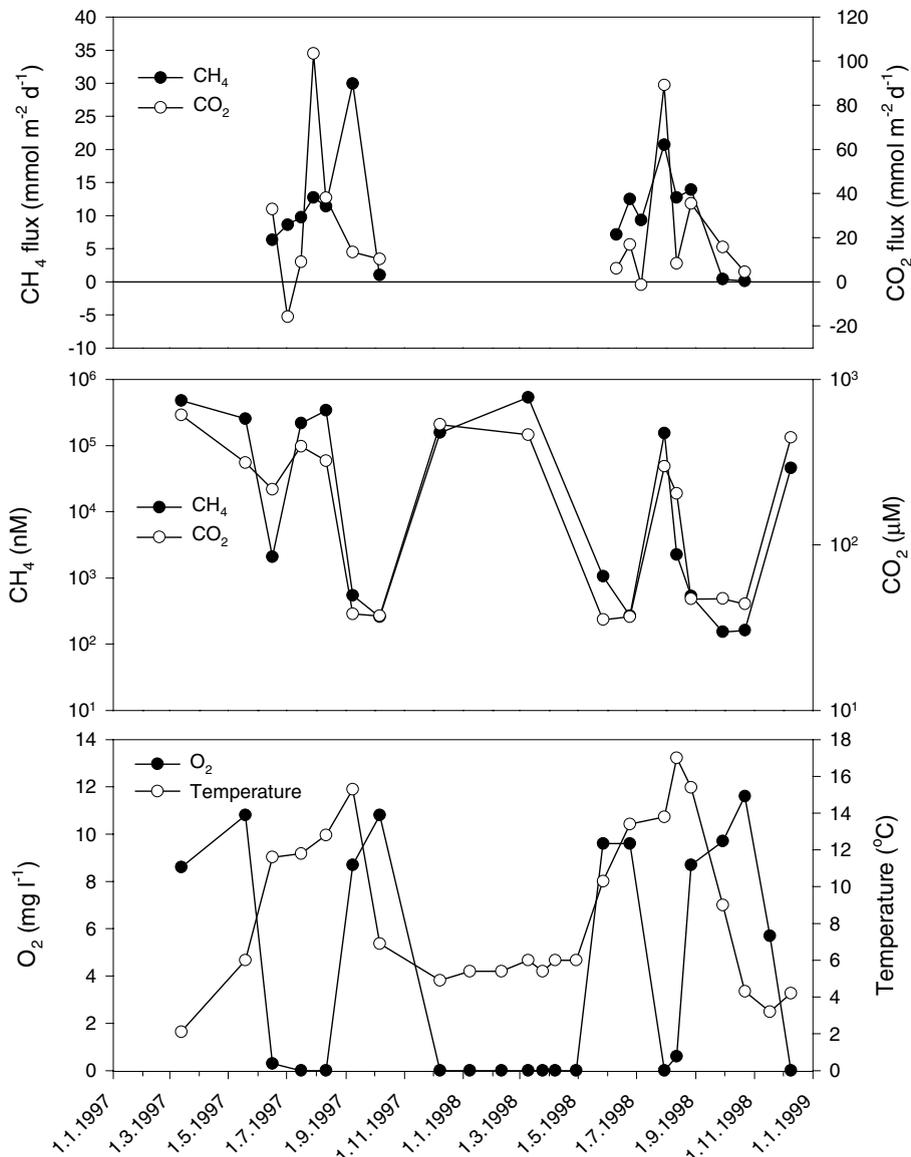


Fig. 2. The seasonal variation in the fluxes of CH_4 and CO_2 at the water–air interface, and the concentrations of dissolved CH_4 , CO_2 and oxygen, and water temperature at a depth of 1 m above the sediment at the deepest station in the highly eutrophic Lake Kevätön in 1997–1998.

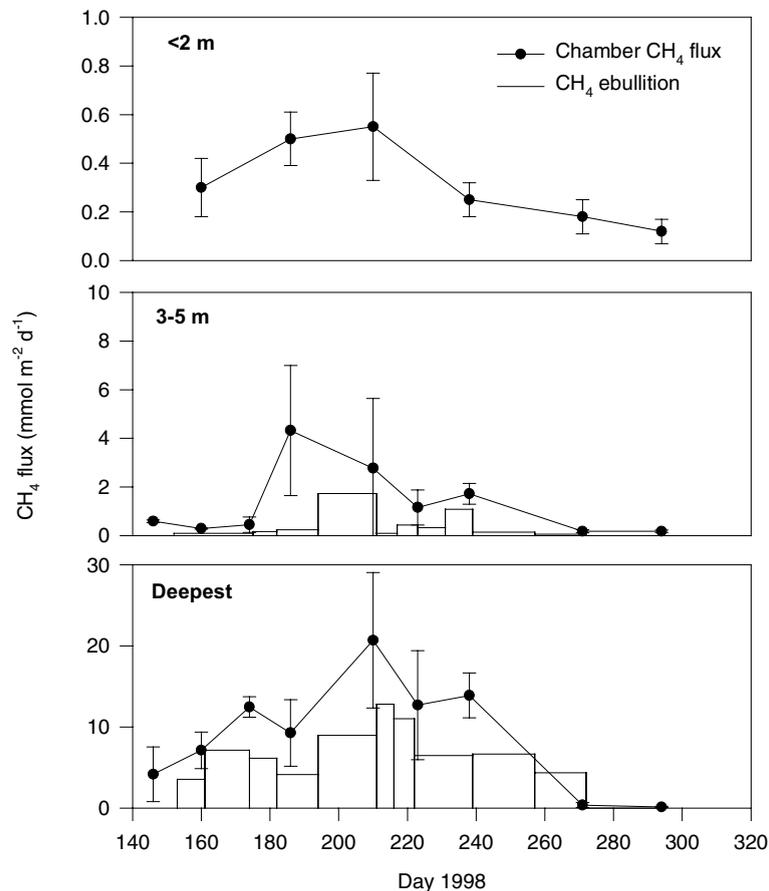


Fig. 3. The CH₄ emissions measured by the chambers and the CH₄ ebullition monitored by the funnel gas collectors at the stations at different depths in the highly eutrophic Lake Kevätön in 1998. Note different scales in each part. Error bars represent standard deviation.

ebullition, it largely bypasses CH₄ oxidation in the uppermost sediment and water column (Kiene, 1991). The relatively high CH₄ emissions from eutrophic Reservoir Lokka (Table 2) were also primarily associated with the anaerobic decomposition of autochthonous, labile organic matter, rather than with decomposition of flooded old peat deposits (Huttunen et al., 2002b). At the stations in Reservoir Lokka, the CH₄ ebullition (seasonal average up to 41 mmol CH₄ m⁻² d⁻¹) was usually higher than the CH₄ fluxes measured by the chambers (Table 2), indicating episodic bubbling in this shallow and exposed reservoir (Huttunen et al., 2002b). There were only low CH₄ emissions from highly eutrophic and oxygen depleted Lake Heinälampi (Table 2). The low CH₄ ebullition rates in the lake suggested low CH₄ production in the sediment (unpublished data). However, the station at the depth of 3.5 m in Lake Heinälampi was not situated in the deepest pelagic zone (Table 1) which could be the zone of the highest CH₄ release based on the results from Lake Kevätön (Fig. 4).

The mesotrophic ponds, oligotrophic Lake Mäkijärvi and eutrophic Lake Vehmasjärvi had the seasonal mean CH₄ emissions from 0.11 to 0.47 mmol m⁻² d⁻¹, similar to the CH₄ release from mesotrophic Reservoir Porttipahta (Table 2). In these lakes, ebullition was not detected (Huttunen et al., 1999, 2002a) and in Reservoir Porttipahta it was negligible (Huttunen et al., 2002b). These low CH₄ emissions are likely associated with: (i) a limitation of the sediment CH₄ production by a low supply of fresh organic matter, and/or (ii) a high capacity of CH₄ oxidation. The shallow ponds were mostly well mixed and oxygenated throughout their depth (Huttunen et al., 2002a), but the thermal stratification and decreased hypolimnetic oxygenation did not enhance to any major extent the CH₄ release from either Lakes Mäkijärvi or Vehmasjärvi during the summer (Huttunen et al., 1999). These results suggest that highly eutrophied boreal lakes can have high CH₄ emissions. In these conditions, the CH₄ ebullition probably has a crucial role in the CH₄ release (see above).

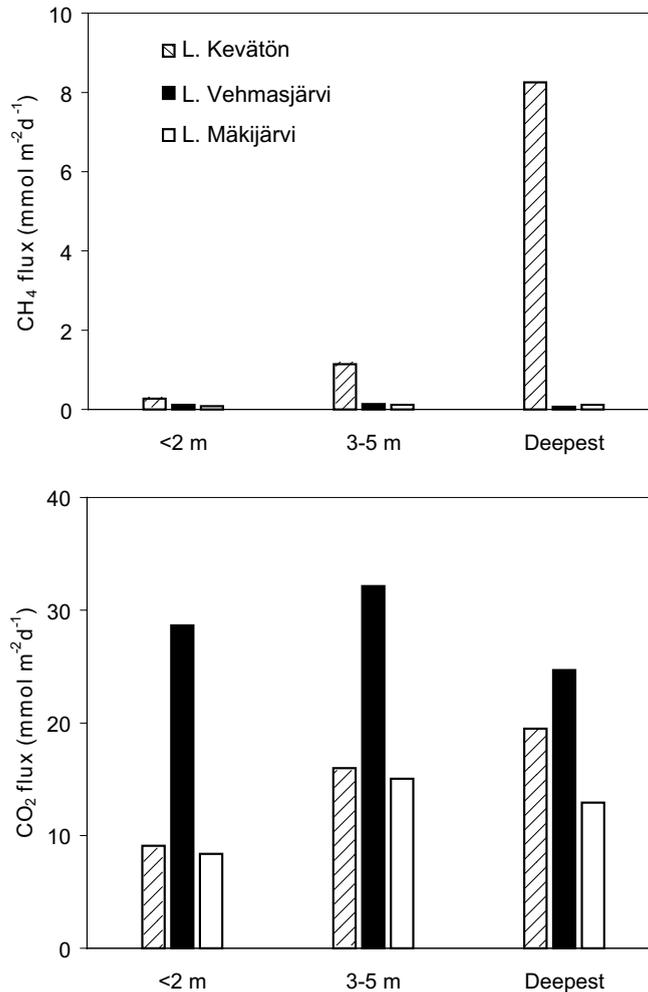


Fig. 4. Seasonal mean CH₄ and CO₂ fluxes (June–October in 1998) from the stations at different depths in the highly eutrophic Lake Kevätön, the eutrophic Lake Vehmasjärvi, and the oligotrophic Lake Mäkijärvi.

The studied ponds, lakes and reservoirs were all net sources of CO₂ to the atmosphere during the open water season (Table 2). The reservoirs had the highest mean CO₂ emissions, but the emissions widely varied between the stations. In Lake Kevätön, there was an increase in the CO₂ release during the summer (Fig. 2), indicating increased mineralization of organic matter. The CO₂ emissions were highly variable from Lake Vehmasjärvi and the eutrophied lakes in the agricultural catchments, but on average, they released more CO₂ than oligotrophic Lake Mäkijärvi and the mesotrophic ponds, which had no significant anthropogenic disturbance (Table 2). The net heterotrophy and CO₂ supersaturation of lakes subsidized by allochthonous C is well documented in lake ecosystems (e.g., Cole, 1999). Therefore, high CO₂ emissions could even be expected from

the humic Lake Vehmasjärvi in the catchment dominated by peatlands and managed forests, and from the humic Jänkäläisenlampi Pond compared with the clear Kotsamolampi Pond. However, although lakes can show uptake of CO₂ from the atmosphere due to high primary production (e.g., Schindler et al., 1972), the highly eutrophic lakes in the Finnish data showed evidence of large CO₂ emissions to the atmosphere in spite of their clearly high primary production. Some temperate lakes in Wisconsin, USA, have retained net heterotrophy in spite of experimental nutrient loading (Cole et al., 2000).

Altogether, the seasonal mean N₂O fluxes were negligible (Table 3). The present results thus suggest that the pelagic regions of shallow boreal lakes are not large sources for atmospheric N₂O during open water season.

Table 3
Mean N₂O fluxes to the atmosphere from some Finnish reservoirs, ponds and lakes during the open water season

Site	Year	Stations	N ₂ O ($\mu\text{mol m}^{-2} \text{d}^{-1}$)		Reference
			Mean	Range ^a	
Reservoir Lokka	1994	5	0.26	−0.39–1.0	Huttunen et al. (2002b)
	1995	5	2.1	−2.0–6.1	Huttunen et al. (2002b)
Reservoir Porttipahta	1995	4	2.6	−0.50–5.8	Huttunen et al. (2002b)
Jänkäläisenlampi Pond	1994	1	0.34		Huttunen et al. (2002a)
Kotsamolampi Pond	1995	1	−0.14		Huttunen et al. (2002a)
Lake Postilampi	1996	1	−0.11		Unpublished data
	1997	1	0.48		Unpublished data
	1998	1	7.0		Huttunen et al. (2000)
Lake Heinälampi	1996	1	−1.8		Unpublished data
Lake Kevätön	1997	3	−0.56	−1.7–0.31	Unpublished data
	1998	3	−0.16	−0.91–0.44	Unpublished data
Lake Vehmasjärvi	1997	2	−0.13	−2.0, 1.7	Unpublished data
	1998	3	5.9	3.0–8.5	Unpublished data
Lake Mäkijärvi	1997	2	−0.24	−1.7, 1.2	Unpublished data
	1998	3	2.1	−3.4–9.6	Unpublished data

^a Mean fluxes for the sites measured with floating chambers, and the range of the mean fluxes at the different sampling stations. The potential fluxes at spring ice melt are not included in the data.

3.2. Greenhouse gas fluxes at spring ice melt

Northern lakes accumulate greenhouse gases in the water column during winter when the gas exchange with the atmosphere is prevented by ice. These gas stores are potentially released to the atmosphere during overturn of the water column after the spring ice melt (Striegl and Michmerhuizen, 1998; Huttunen et al., 2001a, 2003). The potential spring CH₄ emission at the deepest station in Lake Kevätön was 1400 mmol m^{−2} in 1999 (Huttunen et al., 2001a). The deepest pelagic region in a neighboring eutrophied, artificially oxygenated lake (Lake Pöljänjärvi) had potential CH₄ emissions from 0.06 to 19 mmol m^{−2}. This emphasizes the importance of oxygen conditions in the wintertime accumulation of CH₄ in eutrophied boreal lakes (Huttunen et al., 2001a). In Lake Kevätön, oxygen concentration drops after the lake obtains its ice cover, and the accumulation of CH₄ begins (Fig. 2). However, the estimated spring CH₄ emission from Lake Kevätön was only 16 mmol m^{−2} at ice melt in 1999 when the data from the three stations was integrated with depth-versus-volume data for the entire lake, being much less than the point emission at the deepest station. This is due to the shallow morphology of Lake Kevätön (Table 1). The shallow pelagic and infralittoral regions dominate the lake volume and area distribution; the 6–9 m deep region accounts only for 3.4% of the lake area. In Lakes Vehmasjärvi and Mäkijärvi, the spring CH₄ emissions were even lower, 0.7 and 1.6 mmol m^{−2} at the ice melt in 1999, respectively. These data indicate that eutrophied boreal lakes could also show increased CH₄ release at spring ice melt (Huttunen et al., 2001a, 2003).

Carbon dioxide accumulated in the water column during winter (Fig. 2), indicating the potential of release of CO₂ at ice melt. The potential spring CO₂ emissions in Lakes Kevätön, Vehmasjärvi and Mäkijärvi were 840, 710 and 450 mmol m^{−2} at the ice melt in 1999, respectively. The N₂O concentration shows only minor changes in the water column during winter, thus the spring N₂O emissions from shallow boreal lakes are probably low (Huttunen et al., 2001a).

3.3. Annual emissions

The spatial variability in the mean summertime CH₄ and CO₂ emissions from Lakes Kevätön, Vehmasjärvi and Mäkijärvi (Fig. 4) emphasized the importance of the lake morphology in the estimation of the greenhouse gas fluxes for the whole-lake area. The pelagic CH₄ emission from Lake Kevätön was 0.17 mol m^{−2} yr^{−1} during the open water period (June–October, assumed 150 days) in 1998. When the potential spring CH₄ emission is included, the pelagic CH₄ emission totaled 0.18 mol m^{−2} yr^{−1} (open water period 1998 and spring 1999) of which 9% was released in spring. The corresponding annual estimates for Lakes Vehmasjärvi and Mäkijärvi were 0.020 and 0.018 mol CH₄ m^{−2} yr^{−1}, of which the springtime emissions accounted for 4% and 9%, respectively. In Lake Postilampi, where results were available for both the accumulation of dissolved CH₄ in the water column and ebullition during winter, the CH₄ emission at ice melt (0.22–0.49 mol m^{−2}) was estimated to contribute between 22 and 48% to the annual CH₄ release (Huttunen et al., 2003).

The annual CO₂ emissions (open water period 1998 and spring 1999), integrated for the lake area, were 2.9, 5.3 and 2.5 mol m⁻² yr⁻¹ from Lakes Kevätön, Vehmasjärvi and Mäkijärvi, of which the spring emissions accounted for 29%, 13% and 18%, respectively. For these lakes, only 0.4–6% of the annual C loss of 2.5–5.3 mol m⁻² yr⁻¹ to the atmosphere was in the form of CH₄.

4. General discussion and conclusions

4.1. Catchment–lake interactions and the lake CH₄ and CO₂ emissions

Any generalization of the effects of catchment disturbances on the greenhouse gas fluxes in lakes requires data on the fluxes from lakes with different catchment characteristics. Although the number of the lakes in the presented Finnish studies is low, not allowing a statistical treatment of the data, the results may show the potential responses of the aquatic greenhouse gas fluxes to some major anthropogenic stresses threatening boreal lakes. The Finnish data indicated that the highly eutrophied lakes could have high CH₄ emissions both during the open water season and at spring ice melt. The CH₄ concentrations measured from the water column in other 12 Finnish lakes in winter support the importance of the trophic state in the lake CH₄ content; the concentration of dissolved CH₄ in lakes was positively related to total N and P concentrations (Kortelainen et al., 2000). Thus, increasing eutrophication of freshwaters, for example, as a result from intensification of agriculture or climate change (Carpenter et al., 1998; Schindler, 2001), could increase the CH₄ emissions from lakes. This stresses the importance of the controls of nutrient leaching and eutrophication in the mitigation of anthropogenic CH₄ emissions.

All of the ponds and lakes studied in Finland released CO₂, emphasizing the role of boreal lakes as conduits of terrestrial C into the atmosphere. The fueling of the lake CO₂ saturation by allochthonous C has been hypothesized in several studies (e.g., Cole et al., 2000). Recently, Striegl et al. (2001) demonstrated that the CO₂ saturation in Finnish lakes receiving large amounts of dissolved organic C from surrounding peatlands was greater than the CO₂ saturation in lakes set in noncarbonate till and bedrock in Wisconsin and Minnesota, USA. High amounts of organic C are transported to lakes from forests, peatlands and agricultural land (Hope et al., 1996; Müller et al., 1998). Certain land-use practices that increase the leaching of C to lakes would be anticipated to increase the CO₂ emissions from lakes. In the boreal areas, organic matter input to lakes may increase in response to climate change (IPCC, 2001), which would be reflected in the lake CO₂ balances. The leaching of C depends on a complicated interaction of

several environmental factors (e.g., Neff and Asner, 2001), thus there should be a large regional variability in the responses of lake CO₂ balances to climate change.

When reservoirs are constructed, they change the C and N cycling properties in the landscape, including the fluxes of greenhouse gases. In an experimentally flooded wetland in Ontario, Canada, the large CH₄ and CO₂ emissions resulted from the intense decomposition of flooded labile organic matter (Kelly et al., 1997). Although the amount of easily degradable organic matter should decrease with the age of a reservoir, large CH₄ and CO₂ fluxes have still been reported from some reservoirs several decades after flooding (see St. Louis et al., 2000). The eutrophic Reservoir Lokka showed high CH₄ emissions still nearly 30 years after flooding, which suggested that intensive anaerobic decomposition continued in its sediment, and this was likely fueled by fresh autochthonous organic matter (Huttunen et al., 2002b). The bottom of a regulated reservoir, as found for the Reservoir Lokka, can be an important source of nutrients to the primary production, possibly being the key factor for the continuing CH₄ emissions. If this internal nutrient loading maintains high trophic state and oxygen-depleted conditions in the sediment, then intensive CH₄ production may continue for decades (Huttunen et al., 2002b). The erosion of peat from the shallow regions and margins of regulated reservoirs provides not only nutrients but also organic C to the pelagic zone, which additionally contributes to the reservoir C cycle, most likely via CO₂ production. These sources of degradable organic C, and inputs of allochthonous C from the catchment, could explain the large CH₄ and CO₂ emissions recently reported for some old reservoirs.

4.2. N₂O fluxes

The pelagic N₂O fluxes have been negligible in the Finnish studies, although there were some lakes with high N loads. The sediment of Lake Kevätön has showed significant N₂O production in laboratory microcosm studies when nitrate was available (Liikanen, 2002). The N₂O production and emissions would thus seem to require an external nitrate load. The pelagic regions of shallow boreal lakes do not seem to contribute significantly to the atmospheric N₂O budget, which supports previous proposals that freshwater lakes are only moderate sources of N₂O (Mengis et al., 1997).

4.3. Comparison with other ecosystems

The fluxes of CH₄ and CO₂ from Finnish lakes and reservoirs (Table 2) are similar to those reported for temperate lakes, but lower than the emissions from boreal wetland ponds and beaver ponds (Table 4). The net losses of CO₂ to the atmosphere from the Finnish sites point to inputs of allochthonous C from the catchment.

Table 4

Mean CH₄ and CO₂ fluxes to the atmosphere during the open water season from various aquatic ecosystems in temperate and boreal regions

Site (trophic state), ^a location	CH ₄ (mmol m ⁻² d ⁻¹)	CO ₂ (mmol m ⁻² d ⁻¹)	Reference
<i>Reservoirs</i>			
Temperate and boreal reservoirs ^b	0.19–3.37	5.0–78.4	St. Louis et al. (2000)
<i>Temperate and alpine lakes</i>			
Crystal Bog (dys.), Wisconsin, USA	1.24	30.5	Riera et al. (1999)
Trout Bog (dys.), Wisconsin, USA	1.71	45.7	Riera et al. (1999)
Crystal Lake (oligo.), Wisconsin, USA	0.12	0.4	Riera et al. (1999)
Sparkling Lake (meso.), Wisconsin, USA	0.18	5.0	Riera et al. (1999)
Williams Lake, Minnesota, USA	6.3	0.45	Striegl and Michmerhuizen (1998)
Shingobee Lake, Minnesota, USA	8.7	36.5	Striegl and Michmerhuizen (1998)
Red Rock Lake, Colorado, USA	2.94	ND ^c	Smith and Lewis (1992)
Rainbow Lake, Colorado, USA	1.80	ND	Smith and Lewis (1992)
Long Lake, Colorado, USA	0.07	ND	Smith and Lewis (1992)
Pass Lake, Colorado, USA	1.76	ND	Smith and Lewis (1992)
Mirror Lake (oligo.), New Hampshire, USA	ND	6.7–11.5	Cole and Caraco (1998)
Four lakes, Wisconsin, USA ^d	ND	–15–50	Cole et al. (2000)
Priest Pot (hyper.), UK	12	40	Casper et al. (2000)
<i>Boreal ponds</i>			
Three wetland pond groups, Ontario, Canada	6.86–11.2	81.8–261	Hamilton et al. (1994)
Two beaver ponds, Quebec, Canada	0.87–1.0	ND	Ford and Naiman (1988)
Four beaver ponds, Ontario, Canada	8.66–57.3	ND	Bubier et al. (1993)
A beaver pond, Manitoba, Canada	6.79	141	Roulet et al. (1997)

^a Trophic state if given in the reference, dys.—dystrophic, oligo.—oligotrophic, meso.—mesotrophic, hyper.—hypertrophic.

^b The preliminary results from Reservoirs Lokka and Porttipahta, as reviewed by St. Louis et al. (2000), are excluded from the data (see Table 2).

^c Not determined.

^d Includes lakes with food web and nutrient manipulations.

The terrigenous C entering the aquatic ecosystem is released to the atmosphere as CH₄ and/or CO₂, transported downstream within the watercourse or stored in the sediment. In general, the lakes are sources of CO₂ to the atmosphere (e.g., Cole et al., 1994), whereas boreal forests and peatlands have sequestered atmospheric CO₂ during the Holocene and slowly accumulate C in the soil and peat. The annual C emissions from Lakes Kevätön, Vehmasjärvi and Mäkijärvi (2.5–5.3 mol m⁻² yr⁻¹) were of the same order of magnitude than the present observed positive annual C balance (net accumulation) of 2.7–6.1 mol m⁻² yr⁻¹ reported for various microsites in an oligotrophic pine fen in Finland (Alm et al., 1997). An average long-term apparent carbon accumulation rate of 1.5 mol m⁻² yr⁻¹ has been reported for the undrained peatlands in Finland (Turunen et al., 2002). In Finnish upland forest soils, the simulated long-term C accumulation (after initiating fire prevention) is slower, only 0.23 mol m⁻² yr⁻¹ (Liski, 1997). These examples show that the C release from lakes may play an important role in the carbon balance of the catchments in the lake-rich boreal region. For example, lakes cover 10% and 7.6% of the total surface area of Finland and Canada, respectively (Raatikainen and Kuusisto, 1990; Environment Canada, 1998). The preliminary estimates

for the long-term accumulation rates of C in the sediments of Finnish lakes are 0.5 and 0.4 mol m⁻² yr⁻¹ in lake sizes of 0.01–1 and 1–10 km², respectively (Pajunen, 2000). If these rates were applicable for the three Finnish lakes discussed above, the long-term accumulation of C in the sediment would be 7–19% of the annual C-gas loss from small boreal lakes to the atmosphere.

The contribution of CH₄ to the total C emissions from the lakes was small. The seasonal mean CH₄ emissions from the ponds, lakes and reservoirs (0.11–5.1 mmol m⁻² d⁻¹) were lower than the seasonal average emission of 8.6 mmol m⁻² d⁻¹ reported for undrained Finnish fens (minerotrophic peatlands) (Nykänen et al., 1998). However, the lake CH₄ emissions correspond to the average emissions from undrained bogs (ombrotrophic peatlands) (3.1 mmol m⁻² d⁻¹) or drained peatlands (0.44 mmol m⁻² d⁻¹) in Finland (Nykänen et al., 1998). Based on the annual CH₄ emissions estimated for the three above Finnish lakes (see above), the contribution of winter to the annual CH₄ release may be similar in the lakes as in northern terrestrial wetlands (see Huttunen et al., 2003). When ebullition in lakes takes place during winter, the contribution of spring emissions to the annual CH₄ release is even higher (Huttunen et al., 2003).

The lakes in the Finnish gas flux studies were small and shallow and thus were susceptible to eutrophication. The effects of nutrient enrichment on the greenhouse gas fluxes in large lakes may differ from those found in the small lakes. In fact, the wintertime CH₄ and CO₂ concentrations in Finnish lakes were negatively related to the lake area, maximum depth, mean depth and lake volume (Kortelainen et al., 2000). Therefore, the data presented here do not allow an estimation of how nutrient loading and allochthonous C may affect the greenhouse gas exchange in large water bodies. Large lakes could play an important role in the greenhouse gas emissions from Finnish lakes, since lakes larger than 10 km² represent over 60% of the total lake area in the country (Raatikainen and Kuusisto, 1990). Seasonal depth profiles of CH₄, CO₂ and N₂O concentrations have recently been measured in about 200 Finnish lakes covering the entire country which will be used in a more detailed examination on the regulation of the greenhouse gas fluxes in boreal lakes.

The littoral zone may have an important role in total greenhouse gas balances in boreal lake ecosystems. Littoral vegetation and lake-associated wetlands in Finland have generally shown high CH₄ emissions. In the littoral region of Lake Kevätön, the CH₄ emissions have been 0.2–2.4 mol m⁻² during the snow-free period (Juutinen et al., 2003). In Lake Postilampi, the littoral zone and lake-associated wetlands had average CH₄ fluxes from 2.2 to 16 mmol m⁻² d⁻¹ during the summer 1998 (Huttunen et al., 2000). The littoral zone, acting as a buffer zone for nutrient leaching, also releases N₂O. In the summer 1998, the average N₂O emissions from the littoral wetlands of Lake Postilampi were 14–23 μmol m⁻² d⁻¹ (Huttunen et al., 2000), which correspond to the emissions taking place in wetlands treating waste waters (Freeman et al., 1997). Thus, the littoral zone could have importance in the total CH₄ and N₂O emissions from lakes with extensive littoral area. At present, even the total littoral area of Finnish lakes is not known. This area, however, could be large given that the lakes in Finland have a shoreline of about 190 000 km (Kuusisto, 1987).

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References

Alm, J., Talanov, A., Saarnio, S., Silvola, J., Ikkonen, E., Aaltonen, H., Nykänen, H., Martikainen, P.J., 1997.

- Reconstruction of the carbon balance for microsites in a boreal oligotrophic pine fen, Finland. *Oecologia* 110, 423–431.
- Carpenter, S.R., Caraco, N.F., Correll, D.L., Howarth, R.W., Sharpley, A.N., Smith, V.H., 1998. Nonpoint pollution of surface waters with phosphorus and nitrogen. *Ecol. Appl.* 8, 559–568.
- Casper, P., 1992. Methane production in lakes of different trophic state. *Arch. Hydrobiol. Beih. Ergebn. Limnol.* 37, 149–154.
- Casper, P., Maberly, S.C., Hall, G.H., Finlay, B.J., 2000. Fluxes of methane and carbon dioxide from a small productive lake to the atmosphere. *Biogeochemistry* 49, 1–19.
- Cole, J.J., 1999. Aquatic microbiology for ecosystem scientists: new and recycled paradigms in ecological microbiology. *Ecosystems* 2, 215–225.
- Cole, J.J., Caraco, N.F., 1998. Atmospheric exchange of carbon dioxide in a low-wind oligotrophic lake measured by the addition of SF₆. *Limnol. Oceanogr.* 43, 647–656.
- Cole, J.J., Caraco, N.F., Kling, G.W., Kratz, T.K., 1994. Carbon dioxide supersaturation in the surface waters of lakes. *Science* 265, 1568–1570.
- Cole, J.J., Pace, M.L., Carpenter, S.R., Kitchell, J.F., 2000. Persistence of net heterotrophy in lakes during nutrient addition and food web manipulations. *Limnol. Oceanogr.* 45, 1718–1730.
- Cooke, S.E., Prepas, E.E., 1998. Stream phosphorus and nitrogen export from agricultural and forested watersheds on the Boreal Plain. *Can. J. Fish. Aquat. Sci.* 55, 2292–2299.
- Environment Canada, 1998. 1996 in review. An assessment of new research developments relevant to the science of climate change. CO₂/Clim. Report 98-1. Environment Canada, Downsview, Ontario.
- Ford, T.E., Naiman, R.J., 1988. Alteration of carbon cycling by beaver: methane evasion rates from boreal forest streams and rivers. *Can. J. Zool.* 66, 529–533.
- Forsberg, C., Ryding, S.-O., 1980. Eutrophication parameters and trophic state indices in 30 Swedish waste-receiving lakes. *Arch. Hydrobiol.* 89, 189–207.
- Freeman, C., Lock, M.A., Hughes, S., Reynolds, B., Hudson, J.A., 1997. Nitrous oxide emissions and the use of wetlands for water quality amelioration. *Environ. Sci. Technol.* 31, 2438–2440.
- Hamilton, J.D., Kelly, C.A., Rudd, J.W.M., Hesslein, R.H., Roulet, N.T., 1994. Flux to the atmosphere of CH₄ and CO₂ from wetland ponds on the Hudson Bay lowlands (HBLs). *J. Geophys. Res.* 99, 1495–1510.
- Hope, D., Kratz, T.K., Riera, J.L., 1996. Relationship between P_{CO₂} and dissolved organic carbon in northern Wisconsin lakes. *J. Environ. Qual.* 25, 1442–1445.
- Huttunen, J.T., Mäntynen, K., Alm, J., Hammar, T., Silvola, J., Martikainen, P.J., 1999. Pelagic methane emissions from three boreal lakes with different trophic. In: Kuusisto, S., Isoaho, S., Puhakka, J. (Eds.), *Environmental Science, Technology and Policy. Proceedings, Fourth Finnish Conference of Environmental Sciences*, 21–22 May 1999, Tampere, Finland. Water and Environmental Engineering Report 9. Tampere University of Technology, Tampere, Finland, pp. 152–154.
- Huttunen, J.T., Alm, J., Juutinen, S., Silvola, J., Martikainen, P.J., 2000. Greenhouse gas fluxes in a boreal agricultural

- landscape. In: Pietola, L. (Ed.), *Soil Science in the Service of Mankind*. Extended Abstracts of the First Finnish Soil Science Conference, Helsinki 21–22 November 2000, Pro Terra 4. University of Helsinki, Finland, pp. 131–133.
- Huttunen, J.T., Hammar, T., Alm, J., Silvola, J., Martikainen, P.J., 2001a. Greenhouse gases in non-oxygenated and artificially oxygenated eutrophied lakes during winter stratification. *J. Environ. Qual.* 30, 387–394.
- Huttunen, J.T., Lappalainen, K.M., Saarijärvi, E., Väisänen, T., Martikainen, P.J., 2001b. A novel sediment gas sampler and a subsurface gas collector used for measurement of the ebullition of methane and carbon dioxide from a eutrophied lake. *Sci. Total Environ.* 266, 153–158.
- Huttunen, J.T., Väisänen, T.S., Heikkinen, M., Hellsten, S., Nykänen, H., Nenonen, O., Martikainen, P.J., 2002a. Exchange of CO₂, CH₄ and N₂O between the atmosphere and two northern boreal ponds with catchments dominated by peatlands or forests. *Plant Soil* 242, 137–146.
- Huttunen, J.T., Väisänen, T.S., Hellsten, S.K., Heikkinen, M., Nykänen, H., Jungner, H., Niskanen, A., Virtanen, M.O., Lindqvist, O.V., Nenonen, O.S., Martikainen, P.J., 2002b. Fluxes of CH₄, CO₂, and N₂O in hydroelectric reservoirs Lokka and Porttipahta in the northern boreal zone in Finland. *Global Biogeochem. Cycles* 16. Available from doi:10.1029/2000GB001316.
- Huttunen, J.T., Alm, J., Saarijärvi, E., Lappalainen, K.M., Silvola, J., Martikainen, P.J., 2003. Contribution of winter to the annual CH₄ emission from a eutrophied boreal lake. *Chemosphere* 50, 247–250.
- Juutinen, S., Alm, J., Larmola, T., Huttunen, J.T., Morero, M., Saarnio, S., Martikainen, P.J., Silvola, J., 2003. Methane (CH₄) release from littoral wetlands of boreal lakes during an extended flooding period. *Global Change Biol.* 9, 413–424.
- Kauppi, P.E., Posch, M., Hänninen, P., Henttonen, H.M., Ihalainen, A., Lappalainen, E., Starr, M., Tamminen, P., 1997. Carbon reservoirs in peatlands and forests in the boreal regions of Finland. *Silva Fenn.* 31, 13–25.
- Kelly, C.A., Chynoweth, D.P., 1981. The contributions of temperature and of the input of organic matter to controlling rates of sediment methanogenesis. *Limnol. Oceanogr.* 26, 891–897.
- Kelly, C.A., Rudd, J.W.M., Bodaly, R.A., Roulet, N.T., St. Louis, V.L., Heyes, A., Moore, T.R., Schiff, S., Aravena, R., Scott, K.J., Dyck, B., Harris, R., Warner, B., Edwards, G., 1997. Increases in fluxes of greenhouse gases and methyl mercury following flooding of an experimental reservoir. *Environ. Sci. Technol.* 31, 1334–1344.
- Kiene, R.P., 1991. Production and consumption of methane in aquatic systems. In: Rogers, J.E., Whitman, W.B. (Eds.), *Microbial Production and Consumption of Greenhouse Gases: Methane, Nitrogen Oxides and Halomethanes*. American Society for Microbiology, Washington, DC, pp. 111–146.
- Kortelainen, P., Huttunen, J.T., Väisänen, T., Mattsson, T., Karjalainen, P., Martikainen, P.J., 2000. CH₄, CO₂ and N₂O supersaturation in 12 Finnish lakes before and after ice-melt. *Verh. Internat. Verein. Limnol.* 27, 1410–1414.
- Kuusisto, E., 1987. Jokaiselle 54 metriä rantaa. Suomen Kuvalehti, No. 24B. Helsinki, Finland, pp. 134–135.
- Liikanen, A., 2002. *Greenhouse Gas and Nutrient Dynamics in Lake Sediment and Water Column in Changing Environment*, Ph.D. Thesis. In: *Natural and Environmental Sciences*, vol. 147. Kuopio University Publications C, Kuopio, Finland.
- Liski, J., 1997. Carbon Storage of Forest Soils in Finland, PhD Thesis. In: University of Helsinki Department of Forest Ecology Publications, vol. 16. University of Helsinki, Helsinki, Finland.
- Mannio, J., Räike, A., Vuorenmaa, J., 2000. Finnish lake survey 1995: regional characteristics of lake chemistry. *Verh. Internat. Verein. Limnol.* 27, 362–367.
- McCarthy, J.J., 2001. Climate change 2001: Impacts, adaptations, and vulnerability. In: Canziani, O.F., Leary, N.A., Dokken, D.J., White, K.S. (Eds.), *Contribution of Working Group II to the Third Assessment Report of the Intergovernmental Panel on Climate Change (IPCC)*. Cambridge University Press, Cambridge, UK.
- Mengis, M., Gächter, R., Wehrli, B., 1997. Sources and sinks of nitrous oxide (N₂O) in deep lakes. *Biogeochemistry* 38, 281–301.
- Müller, B., Lotter, A.F., Sturm, M., Ammann, A., 1998. Influence of catchment quality and altitude on the water and sediment composition of 68 small lakes in Central Europe. *Aquat. Sci.* 60, 316–337.
- Neff, J.C., Asner, G.P., 2001. Dissolved organic carbon in terrestrial ecosystems: synthesis and a model. *Ecosystems* 4, 29–48.
- Nykänen, H., Alm, J., Silvola, J., Tolonen, K., Martikainen, P.J., 1998. Methane fluxes on boreal peatlands of different fertility and the effect of long-term experimental lowering of the water table on flux rates. *Global Biogeochem. Cycles* 12, 53–69.
- Pajunen, H., 2000. Lake sediments: their carbon store and related accumulation rates. In: Pajunen, H. (Ed.), *Carbon in Finnish Lake Sediments*. Geological Survey of Finland, Espoo, Finland, pp. 39–69, Special Paper 29.
- Raatikainen, M., Kuusisto, E., 1990. Suomen järvien lukumäärä ja pinta-ala. *Terra* 102, 97–110.
- Riera, J.L., Schindler, J.E., Kratz, T.K., 1999. Seasonal dynamics of carbon dioxide and methane in two clear-water lakes and two bog lakes in northern Wisconsin, USA. *Can. J. Fish. Aquat. Sci.* 56, 265–274.
- Roulet, N.T., Crill, P.M., Comer, N.T., Dove, A., Bourbonniere, R.A., 1997. CO₂ and CH₄ flux between a boreal beaver pond and the atmosphere. *J. Geophys. Res.* 102, 29313–29319.
- Saarnisto, M., 2000. Shoreline displacement and emergence of lake basins. In: Pajunen, H. (Ed.), *Carbon in Finnish Lake Sediments*. Geological Survey of Finland, Espoo, Finland, pp. 25–34, Special Paper 29.
- Schindler, D.W., 2001. The cumulative effects of climate warming and other human stresses on Canadian freshwaters in the new millennium. *Can. J. Fish. Aquat. Sci.* 58, 18–29.
- Schindler, D.W., Brunskill, G.J., Emerson, S., Broeker, W.S., Peng, T-H., 1972. Atmospheric carbon dioxide: its role in maintaining phytoplankton standing crops. *Science* 177, 1192–1194.
- Seitzinger, S., 1990. Denitrification in aquatic sediments. In: Revsbech, N.P., Sørensen, J. (Eds.), *Denitrification in Soil and Sediment*. Plenum Press, New York, pp. 301–322.

- [Smith, L.K., Lewis Jr., W.M., 1992. Seasonality of methane emissions from five lakes and associated wetlands of the Colorado Rockies. *Global Biogeochem. Cycles* 6, 323–338.](#)
- St. Louis, V.L., Kelly, C.A., Duchemin, E., Rudd, J.W.M., Rosenberg, D.M., 2000. Reservoir surfaces as sources of greenhouse gases to the atmosphere: a global estimate. *Bioscience* 50, 766–775.
- [Striegl, R.G., Michmerhuizen, C.M., 1998. Hydrologic influence on methane and carbon dioxide dynamics at two north-central Minnesota lakes. *Limnol. Oceanogr.* 43, 1519–1529.](#)
- [Striegl, R.G., Kortelainen, P., Chanton, J.P., Wickland, K.P., Bugna, G.C., Rantakari, M., 2001. Carbon dioxide partial pressure and ¹³C content of north temperate and boreal lakes at spring ice melt. *Limnol. Oceanogr.* 46, 941–945.](#)
- [Turunen, J., Tomppo, E., Tolonen, K., Reinikainen, A., 2002. Estimating carbon accumulation rates of undrained mires in Finland—application to boreal and subarctic regions. *Holocene* 12, 79–90.](#)