Irina Bergström

Carbon gas fluxes from boreal aquatic sediments

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Carbon gas fluxes from boreal aquatic sediments

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“Nowhere can one see more clearly illustrated what may be called the sensibility of such an organic complex, expressed by the fact that whatever affects any species belonging to it, must have its influence of some sort upon the whole assemblage. He will thus be made to see the impossibility of studying completely any form out of relation to the other forms; the necessity for taking a comprehensive survey of the whole as a condition to a satisfactory understanding of any part.”

S.A. Forbes 1887: The Lake as a Microcosm.
List of original publications

This study synthesizes the results of the following original publications, which are referred to in the text by their Roman numerals. The author’s contribution is described separately for each article. In addition, some previously unpublished results, tables and figures are included in this study.


Author’s contributions

**Paper I**
I. Bergström was partly responsible for planning the study and fully responsible for the field work, laboratory analyses, processing and interpreting of the data and writing the paper.

**Paper II**
I. Bergström was responsible for the field work, laboratory analyses and processing the benthic respiration data, partly responsible for interpreting the benthic respiration data and she participated in preparation of the manuscript.

**Paper III**
I. Bergström was partly responsible for planning of the study, field work, laboratory analyses and for processing and interpreting the methane production and consumption data. She participated in writing the manuscript.

**Paper IV**
I. Bergström participated in the planning of the study, field work and processing the results, and she participated in writing the manuscript. T. Käki and S. Mäkelä participated in the field work.

**Paper V**
I. Bergström was fully responsible for planning the study, performing the data analysis, interpreting the data, and writing the paper. S. Mäkelä provided the vegetation data and participated in preparation of the manuscript.
List of abbreviations and unit conversion factors

AFDW  ash-free dry weight
C    carbon
CH\textsubscript{4}  methane
CO\textsubscript{2}  carbon dioxide
DA  dark-anoxic incubation
DIC  dissolved inorganic carbon
DM  dry mass, dry weight
FID  flame ionization detector
gs  growing season
LO  light-oxic incubation
LOI  loss on ignition
MF  mean fetch
MM  mineral mass, mineral weight
NEE  net ecosystem exchange
NEP  net ecosystem production
NPP  net primary production
O\textsubscript{2}  oxygen
OM  organic mass, organic weight
Q\textsubscript{10}  the proportional increase in gas production or emission rate for a temperature increase of 10 °C, also called temperature sensitivity
R  ecosystem respiration
RQ  respiratory quotient, CO\textsubscript{2}/O\textsubscript{2} (mol); RQ = 0.85 (Wetzel 2001)
T  temperature
VegSL  Vegetation Study Lakes
WM  wet mass, wet weight

1.0 mg CO\textsubscript{2}  = 0.27 mg C
1.0 ml CO\textsubscript{2}  = 0.54 mg C
1.0 mmol CO\textsubscript{2}  = 12 mg C
1.0 mg CH\textsubscript{4}  = 0.75 mg C
1.0 ml CH\textsubscript{4}  = 0.69 mg C
1.0 mmol CH\textsubscript{4}  = 12 mg C
The carbon dioxide (CO$_2$) and methane (CH$_4$) fluxes from aquatic sediments have recently received considerable interest because of the role of these gases in enhancing climate warming. CO$_2$ is the main end product of aerobic respiration and CH$_4$ is produced in large amounts under anaerobic conditions. Shallow, vegetated sediments are an important source of both gases. CH$_4$ may be transported via rhizomes and aerenchymal tissues of aquatic plants from the sediment to the atmosphere, thus avoiding oxidation in the aerated sediment surface and water column. Temperature is known to be a key factor affecting benthic CO$_2$ and CH$_4$ flux rates, but the interplay between other factors that may affect the fluxes from sediments is still poorly known. In order to study the spatial and temporal variability of carbon gas fluxes in boreal aquatic sediments, the area-based CO$_2$ production rates in lake and brackish water sediments and CH$_4$ emissions in vegetated lake littorals were measured in this work. The effects of temperature, sediment quality, plant species, zoobenthos and seasonal variation on flux rates were also estimated. The range of CO$_2$ production rates measured in the field was 0.1–12.0 mg C m$^{-2}$ h$^{-1}$ and that of CH$_4$ emission rates 0–14.3 mg C m$^{-2}$ h$^{-1}$. When incubated at elevated temperatures (up to 30°C) in the laboratory, the CO$_2$ production rates increased up to 70 mg C m$^{-2}$ h$^{-1}$. Temperature explained 70–94% of the temporal variation in the CO$_2$ production in lake sites and 51% in a brackish water site. In the lake mesocosm, temperature explained 50–90% of the variation of CH$_4$ emission. By contrast, CH$_4$ oxidation rate was not dependent on temperature. The CH$_4$ fluxes through the plants of six emergent and floating-leaved plant species were studied in the field (temperature range 20.4–24.9 °C). Stands of the emergent macrophyte Phragmites australis emitted the largest amounts of CH$_4$ (mean emission 13.9 ± 4.0 (SD) mg C m$^{-2}$ h$^{-1}$), the mean emission rate being correlated with mean net primary production (NPP) and mean solar radiation. In the stands of floating-leaved Nuphar lutea the mean CH$_4$ efflux (0.5 ± 0.1 (SD) mg C m$^{-2}$ h$^{-1}$) was negatively correlated with mean fetch and positively with percentage cover of leaves on the water surface. On a regional level, stands of the emergents P. australis and Equisetum fluviatile emitted 32% more CH$_4$ than natural open peatland during the growing season, although their areal coverage in the study region was only 41% of that of peatland area. Climate warming will presumably increase the carbon gas emission from vegetated littorals. The model-based estimated increase of CO$_2$ production rate in June was 29% and for CH$_4$ emissions as much as 65% for the time interval of 110 years from 1961–1990 to 2071–2100. The results indicate that carbon gas fluxes from aquatic sediments, especially from vegetated littorals, are significant at the landscape level. They are linked to temperature but also to several other interacting factors such as e.g. water and bottom quality and ecosystem composition. Detailed investigation of the overall links between the causes and effects is urgently needed in order to understand and predict the changes caused by warming climate.
1 Introduction

1.1 Aquatic sediments as a source of carbon gases

In lakes and coastal regions, especially in shallow and littoral areas, much of the overall metabolism takes place in aquatic sediments (e.g. den Heyer and Kalff 1998, Wetzel 2001, Gazeau et al. 2004, Pace and Prairie 2005). Sediments are a significant source of carbon dioxide (CO$_2$) and methane (CH$_4$). These gases are the two major end products of respiratory carbon metabolism, CO$_2$ mainly being the end product of aerobic respiration and CH$_4$ being produced in large amounts in anoxic layers of the sediment as a final step in the degradation of organic carbon by methanogenic organisms, archaea (e.g. Liikanen et al. 2003b, King 2005). If CH$_4$ diffuses into the oxic parts of the sediment, or into the aerobic water overlying the sediment, it may be further oxidized into CO$_2$ by methanotrophic bacteria. If the gas evades from the sediment via plant stems or by bubbling, it transfers directly to the atmosphere.

The decomposition and mineralisation processes, characteristic for sediments, have attracted only limited interest before (see e.g. Williams and del Giorgio 2005), but recently the carbon gases have come into focus owing to their role in climate warming (Forster et al. 2007). In randomly selected boreal Finnish lakes an average of 21 times more carbon has been estimated to be transported to the atmosphere than permanently buried in sediments (Kortelainen et al. 2006). In a study of lakes in the Northern Highland area of Wisconsin, ebullition, diffusive emission and burial accounted for 65, 24 and 12% of open water CH$_4$ emission, respectively (Bastviken et al. 2004). On a global scale, 2–10 times more carbon has been estimated to be lost to the atmosphere by evasion than is buried in the sediment (Alin and Johnson 2007, Cole et al. 2007, Tranvik et al. 2009), and there is currently much discussion about how the proportions will change when temperature rises and what are the controls of the change (e.g. Kortelainen et al. 2004, Tranvik et al. 2009, Gudasz et al. 2010, Kosten et al. 2010).

There is not much information on coastal benthic mineralization rates in Northern Baltic region, but estuaries generally exhibit high metabolic rates. Comprehensive global evaluation of the respiration rates of benthic coastal ecosystems is lacking, too (Middelburg et al. 2005). However, Gazeau et al. (2004) estimate that in European coastal zone, benthic community respiration consumes approximately 40% of the pelagic organic matter production.

Mineralisation processes in aquatic ecosystems are controlled by the availability of oxygen, nutrients, and the quality and the amount of organic matter, together with temperature, light and other physical factors (Wetzel 2001, Middelburg et al. 2005). On the other hand, biotic activity itself affects the quality of the abiotic environment and may alter the relative quantities of compounds necessary to the biota. Moreover, biological, chemical and physical variables affecting carbon gas production and emission from aquatic sediments may vary with integrative factors, such as season, habitat type, water depth and other site- or lake-specific characteristics, which makes the interplay exceedingly complex.

The effect of temperature on sediment CO$_2$ and CH$_4$ fluxes has recently been the focus of several studies, and temperature is regarded as one of the main factors affecting the rate of mineralization (Zeikus and Winfrey 1976, Kelly and Glynoweth 1981, van Es 1982, Gudasz et al. 2010, Zhu et al. 2010). However, synergistic effects of temperature with other variables remain more obscure and are less frequently studied. den Heyer and Kalff (1998) concluded that although the effect of temperature was probably the principal determinant of carbon mineralisation rates (CO$_2$ production and CH$_4$ emission), water depth did explain some of the variability and consequently was more than a simple surrogate for temperature. Similarly, maximum depth was an important driver for CO$_2$ and CH$_4$ evasion from randomly selected Finnish lakes (Kortelainen et al. 2006, Juutinen et al. 2009), whereas temperature was not significantly correlated with CO$_2$ fluxes (Rantakari...
Aquatic vegetation has an important role in carbon transfers in the littoral, and vegetation stands interact with the sediment biota in many ways. The littoral plants consume carbon as CO₂ for primary production, incorporate it in the biomass and produce it when respiring. The decaying littoral plant biomass sinks onto the bottom and is an important substrate for benthic decomposers that produce CO₂ and, in anaerobic layers of the sediment, also CH₄ in their respiratory processes (e.g. Wetzel 2001). Emergent and floating-leaved plants are significant conduits that transport CH₄ and other gases from the anoxic sediment via aerenchymal tissues directly to the atmosphere (Dacey and Klug 1979, Sebacher et al. 1985). It has been estimated that more than 90% of the CH₄ flux from the anoxic littoral sediment to the atmosphere is mediated by plants (Schutz et al. 1989, van der Nat and Middelburg 1998a, Joabsson et al. 1999).

The wetland plants also have mechanisms to transfer oxygen via aerenchymal tissues to the rhizomes and thus they aerate the anaerobic sediment layers (Grosse et al. 1996), where oxygen facilitates the oxidation of CH₄ by aerobic methanotrophs in otherwise anaerobic environments (Epp and Chanton 1993, King 1996). They also transport fresh carbon compounds to anoxic parts of the sediment (van Veen et al. 1989, Chanton et al. 1995, Laanbroek 2010). Seasonal variation and interspecific differences exist in the rhizospheric oxidation, depending on the growth phase and gas transport mechanism of the plant (Moorehead and Reddy 1988, Calhoun and King 1997, van der Nat and Middelburg 1998b). Frenzel (2000) analyzed in detail the factors affecting the oxidation and found that the areas vegetated by wetland plants may be responsible for as much as 90% of the total CH₄ oxidation from a wetland.

Emergent macrophytes are superior over floating-leaved and submerged macrophytes with respect to their capacity to emit CH₄ to the atmosphere, presumably because of their continuous access to the atmosphere linked to their adaptation to live under partly oxygen-limited conditions (Laanbroek 2010). Common reed (Phragmites australis) and water horsetail (Equisetum fluviatile) have been intensively studied in this respect. P. australis is a cosmopolitan and major species in much of the land-water ecotone in Europe. It has a pressurized convective flow mechanism and is known to have particularly high rates of convective flow during daytime; its wide monospecific stands may be a major source of carbon gas emissions in lake littorals as well as in other wetland ecosystems (Brix et al. 1996). E. fluviatile is a common cryptogam in the boreal zone, especially in oligotrophic lakes, where it also forms large monospecific stands on varying bottom types (Toivonen and Lappalainen 1980). Although presenting a less effective diffusive mode of gas flow mechanism, E. fluviatile has also been the subject of several greenhouse gas studies as a widely distributed and dominant macrophyte in freshwater habitats. Both are common emergents in lake littorals in Finland (Toivonen and Huttunen 1995, Mäkelä et al. 2004). The CO₂ and CH₄ fluxes from P. australis and E. fluviatile stands and the contributing factors have been studied extensively both in Finland (e.g. Kairesalo 1983, Hyvönen et al. 1998, Ojala et al. 2000, Käki et

### 1.3 Regional carbon gas fluxes from lake littorals

On a landscape scale, lakes play an important role in the regional carbon budget, even if they occupy only a small fraction of the landscape (Kortelainen et al. 2004, Prairie 2008). They receive much dissolved organic carbon from the terrestrial landscape (Kortelainen 1993, Rantakari et al. 2010), and its accumulation in water bodies and subsequent transformations by the microbial community may significantly affect the metabolic balance of the lake ecosystems, simultaneously releasing CO$_2$ and CH$_4$ to the atmosphere and burying organic carbon in lake sediments. The global and regional role of lakes has been studied intensively in the 2000s as it has become obvious that lakes have a significant role in the global carbon cycle, net carbon fluxes over prolonged time being greater per unit area than in much of the surrounding land (Algesten et al. 2003, Kortelainen et al. 2006, Cole et al. 2007, Battin et al. 2009). Bastviken et al. (2011) estimated that global CH$_4$ emissions from lakes expressed as CO$_2$ equivalents correspond to at least 25% of the estimated terrestrial greenhouse gas sink.

Freshwater wetlands and vegetated shallow littorals are an important part of lakes and they may emit considerable amounts CH$_4$ per unit area into the atmosphere. Roehm (2005) estimated, based on the literature, that mean rates of CO$_2$ and CH$_4$ respiration from freshwater wetlands range between 0.1 and 0.6 mol C m$^{-2}$ d$^{-1}$ (50–300 mg C m$^{-2}$ h$^{-1}$) and 0.6 and 12 mmol C m$^{-2}$ d$^{-1}$ (0.3–6 mg C m$^{-2}$ h$^{-1}$), respectively. Juutinen et al. (2003) estimated that mean CH$_4$ fluxes from three Finnish mid-boreal lakes were 0.08–0.42 mol m$^{-2}$ (1–5 g C m$^{-2}$) during the ice-free season and that 66–77% of the CH$_4$ was released from the littoral zone. The boreal lakes are mostly shallow and thus the littoral area covers a significant part of the total lake area. The water depth under 1.5 m is often considered as the maximum depth for emergent macrophyte growth (Wetzel 2001). In Finland, 16% (5300 km$^2$) of the total lake area has a water depth of less than 1.5 m and for the lakes with a total area less than 0.5 km$^2$ the proportion is 43% (1600 km$^2$) (Kuusisto and Hakala 2007). In the boreal zone, the regional role of littoral in carbon gas fluxes is significant also because of long, winding lake shorelines often with wetland margins. However, in regional and global estimates lake littorals have still often been underestimated as a source of atmospheric carbon (Bastviken et al. 2011).

### 1.4 Climate warming and aquatic lake sediments

Since climate change became one of the most serious environmental threats towards the end of the 20$^{th}$ century, the carbon gas fluxes in natural environments have also attracted much interest. The warming climate has important effects on lake and watershed metabolism, and especially during periods when the water is
Carbon gas fluxes from boreal aquatic sediments

cold, even small changes in temperature may have a great effect on mineralisation rates in the sediment (Pace and Prairie 2005). During the past 100 years, global warming has delayed the winter freeze-up and advanced the lake ice break-up times over the northern hemisphere by 5.8 and 6.5 days, respectively (Magnuson et al. 2000). The average trend for a shorter duration of ice cover in southern Finland for the period 1886–2002 is 16.8 days (Korhonen 2006). This lengthens the period when carbon gases can easily escape to the atmosphere. Moreover, recent studies (e.g. Gudasz et al. 2010, Kosten et al. 2010) suggest that cool lakes, such as lakes in the boreal zone, start to emit more CO₂ and CH₄ when they warm up because of climate change.

Not all changes in lake respiration rates due to the changing climate are direct consequences of increasing global temperature. Climate warming is also expected to change precipitation patterns and it has been suggested that changes in hydrology may be even more important than rising temperature in determining carbon mineralization and CO₂ emissions from lakes. These changes may result in shifts in organic matter loading from the drainage basins, which in turn would influence lake water and sediment fluxes (Algesten et al. 2003, 2005). The resulting altered flooding patterns would cause changes in carbon gas emissions in lake littorals (Juutinen et al. 2001, Larmola et al. 2004). Yvon-Durocher et al. (2010, 2011) suggested that the metabolic balance between photosynthesis and respiration will also shift in freshwater ecosystems, altering their capacity to absorb CO₂ and increasing the proportion of primary production emitted as CH₄.

1.5 Objectives of this study

The aim of this study was to elucidate the carbon gas fluxes from aquatic sediments, with the main emphasis on vegetated lake littorals, and to consider physical, chemical and biological factors that might be the major players regulating gas transfers from sediment to water and air. In papers I, II and III, the relationship between temperature and gas fluxes was studied in order to determine how the temperature response of the benthic communities varies seasonally, spatially with depth and with the sediment characteristics. The oxidized proportion of CH₄ was also defined, as well as the factors controlling oxidation, in experimental lake mesocosms with stands of emergent macrophyte E. fluviatile. In paper IV, the main focus was on spatial variation of CH₄ emissions within littoral vegetation in a boreal lake, and the effects of plant species and other factors, e.g. solar radiation, mean fetch and plant biomass, on the emissions. Temperature did not vary much in this study, thus facilitating the examination of the other factors, the effect of which might otherwise have been hidden. In paper V the scope was widened from individual study sites and lakes to the whole lake population within the larger region in southern Finland, in order to assess the regional significance of vegetated lake littoral areas on natural CH₄ emissions and the role of different plant species. The main objectives and key questions in the studies included in this summary are presented in Table 1.

2 Materials and methods

2.1 Study sites, lakes and regions

Carbon gas fluxes from aquatic sediments were estimated at site, lake and regional levels and by performing mesocosm and laboratory scale experiments. Freshwater studies (papers I, III, IV, V) were performed in southern Finland, within the drainage area of the river Kokemäenjoki (total area 27 046 km², lake proportion 12%). The brackish water study (paper II) was conducted offshore from Tvärminne on the southwest coast of Finland. All study sites, lakes and regions are shown in Fig. 1. For a summary of the data used, see Table 2.

In order to be able to compare the carbon escaping as CO₂ and CH₄ gases from the aquatic sediments in different habitats, and the carbon escaping as gas and stored in biomass, all carbon gas fluxes and biomasses, as well as model parameters used in this study are given as carbon. The conversion factors used to convert the units from the original papers (papers I–V) to
Table 1. Main objectives and key questions in the papers included in the thesis.

<table>
<thead>
<tr>
<th>Paper</th>
<th>Main objectives</th>
<th>Key questions</th>
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<tbody>
<tr>
<td>I</td>
<td>To investigate the role of temperature and sediment variables in lake sediment community respiration (CO₂ production) in different seasons and parts of a lake.</td>
<td>How does the lake sediment community respiration (CO₂ production) respond to temperature changes? What are the effects of season, water depth and sediment characteristics?</td>
</tr>
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<td>II</td>
<td>To study the community respiration (O₂ consumption; converted to CO₂ production) of the brackish-water sediment community and the main factors affecting it.</td>
<td>What is the level of annual benthic respiration? What is the effect of temperature on total benthic metabolism? What is the effect of organic input and the role of Monoporeia (Pontoporeia) affinis on the benthic respiration?</td>
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<tr>
<td>III</td>
<td>To estimate the CH₄ fluxes in the littoral Equisetum fluviatile stand growing on organic sediment and on sand bottom and to study factors affecting the fluxes.</td>
<td>To what extent are plant-mediated CH₄ emissions from Equisetum fluviatile stands due to variation in temperature, bottom type and rhizospheric CH₄ oxidation? What other factors affect the emission?</td>
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<tr>
<td>IV</td>
<td>To study the spatial variation of CH₄ efflux in different littoral vegetation stands of a meso-eutrophic lake.</td>
<td>How are the species composition of macrophytes and other environmental variables related to spatial variation of CH₄ efflux in a lake?</td>
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<td>V</td>
<td>To scale up and produce a regional estimate of CH₄ efflux from the vegetated littoral for a lake population in southern Finland. To compare this with the flux from natural open peatland of the same region.</td>
<td>What is the regional CH₄ flux and its annual variation in the littorals with zones of Equisetum fluviatile, Phragmites australis and some other aquatic macrophytes? Do natural open peatlands produce more or less CH₄ than Equisetum fluviatile and Phragmites australis littorals?</td>
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Table 2. Summary of the data used in the summary and in the papers I–V

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<td>Lake-level</td>
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<td>Vegetated littoral</td>
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Carbon gas fluxes from boreal aquatic sediments

... carbon units are given in the List of abbreviations and unit conversion factors.

The field and laboratory experiments on benthic CO$_2$ production (paper I) were conducted in Lake Pääjärvi (61°04′N, 25°08′E; Fig. 1), a boreal, meso-oligotrophic lake with a lake surface area of 13.5 km$^2$ and mean and maximum depths of 14.4 and 85.5 m, respectively. Vegetated littoral covers 3% of the lake surface. Intensive hydrological, physical, chemical and ecological studies have been conducted in the lake and its catchment area since the 1960s (e.g. Kansanen et al. 1974, Ruuhijärvi 1974, Sarvala et al. 1981, 1982, Kairesalo 1983, Saloranta et al. 2009, Vehmaa and Salonen 2009).

A brackish water study of benthic O$_2$ consumption (CO$_2$ production) (paper II) was conducted on a soft-bottom site, located in Tvärminne Storfjärd (59°51′22″N, 23°15′41″E; Fig. 1). The hydrography and general biology of the area at the time of the study, 1980, is presented e.g. in Niemi (1975) and Hälfors et al. (1983).

Sediment material for the mesocosm study on littoral CH$_4$ emission and oxidation (paper III) was drawn from Pappilanlahti Bay of Lake Pääjärvi (Fig. 1). Field measurements of CH$_4$ emission in macrophyte stands of different species were performed in vegetated littoral of Lake Ekojärvi (61°11′N, 24°57′E; Fig. 1; paper IV), a small, polyhumic headwater lake with a

Figure 1. Study areas and sites. In the Regional study area, the Vegetation Study Lakes are dark grey. In Lake Pääjärvi, filled circles denote study sites and a filled square denotes the lakeside mesocosm study site. The study area of Lake Ekojärvi is designated with an open square. Background map of Regional study area: ©National Land Survey of Finland, license no. 7/MYY/06; map of Lake Pääjärvi: ©University of Helsinki, Lammi Biological Station 1982.
The regional CH₄ emission study on lake littorals (paper V) covered all lakes (619 in total) lying within the area delimited by the coordinates 60°57’N, 61°22´N, 24°25´E and 25°15´E (Fig. 1). The total area of the study region was 1600 km², lake area 245 km², lake shoreline length 1165 km and lake and peatland proportions 16% and 10%, respectively. Littoral vegetation was mapped in 50 lakes by Mäkelä et al. (2004). Total area of the mapped lakes was 182 km², comprising 74% of the total lake surface area of the study region, and lake shoreline length was 749 km, which was 64% of the total shoreline length of all lakes in the region. Among the most common species forming stands in the lakes were the emergents P. australis and E. fluviatile and floating-leaved N. lutea. A more detailed description of the vegetation data is given in Mäkelä et al. (2004). The climatic conditions in the lake study region are given in paper V.

2.2 The effect of temperature and sediment quality on benthic CO₂ production — Lake Pääjärvi

The seasonal and site specific CO₂ production (paper I) was measured in the field once per season (winter stratification, spring turnover, summer stratification and autumn turnover) in 1977 in the Ronninlahti Bay of Lake Pääjärvi from depths of 1.2 and 2.5 m (littoral), 5 and 10 m (profundal, summer metalimnion area) and 20 and 40 m (profundal, summer hypolimnion area) (Fig. 1). Temperature just above the sediment surface was used in the calculations. The sediment samples for all CO₂ production measurements were taken with a 15.2 cm² tube corer so that a water volume of 200–300 cm³ was left over the sediment. In the field incubations, the darkened sediment cores were settled back onto the place of sampling at the same depth just above the sediment. In the laboratory, the cores were incubated in the dark at constant temperature (1, 8, 15, 21, 23 or 30 °C for winter cores, 2, 10, 15, 21, 26 or 30 °C for early summer cores and 6, 11, 16, 20, 25 or 30 °C for late summer cores). The incubation times in the field and laboratory experiments varied, depending on incubation temperature, from some hours (high temperature; summer; littoral sediment) up to 5 days (low temperature; winter; deep profundal sediment).

CO₂ production rate of the sediment was estimated with an infra-red gas analyzer by determining dissolved inorganic carbon (DIC) concentration in the water overlying the sediment with the method described by Salonen (1981), in which CO₂ was liberated by acidification and bubbling. CO₂ production rates were calculated from the linear part of the DIC accumulation curve. A detailed description of the method is given in Bergström and Salonen (1979).

After the field CO₂ production measurements, the wet (WM), dry (DM), mineral (MM), and organic (OM) masses of the topmost 2 cm layer of sediment were determined in each core. The whole-lake annual estimate for CO₂ production of the sediment was based on seasonal temperature and CO₂ production data obtained from the field measurements at Ronninlahti Bay. The durations of the thermal seasons were calculated from data of the Finnish Meteorological Institute weather station (Lahti, Laune; Ilmatieteen laitos 1977). The areas of different depth zones in Lake Pääjärvi were estimated using the digitized bathymetric map of Lake Pääjärvi (©University of Helsinki, Lammi Biological Station 1982).

The increase of benthic CO₂ production in future conditions of warming climate (years 2071–2100) was estimated using the model simulations for the impacts of projected climate change on the thermodynamics of Lake Pääjärvi (MyLake model; T. Saloranta unpubl. data and Saloranta et al. 2009) and applying the
Carbon gas fluxes from boreal aquatic sediments

2.3 Benthic CO$_2$ production in brackish water — Tvärminne Storfjärd

In the study on brackish water sediment respiration (paper II), sediment cores, with about 100 cm$^3$ of overlying water, were collected from 7 May to 10 December 1980 (23 samplings) at a 26 m soft-bottom site with a 15.2 cm$^2$ bottom corer. The cores were incubated for 3–5 hours in dark at field temperature in the laboratory (incubation time depending on temperature) for the determination of total benthic respiration. In the original study, benthic respiration was initially measured as the O$_2$ decrease in the water overlying the sediment in intact sediment cores. The respiration in the water itself was assumed to be insignificant during incubation. O$_2$ concentration of the water was determined before and after incubation using the modified micro-Winkler technique of Fox and Wingfield (1938). The initial O$_2$ concentration in the water overlying the sediment cores varied generally between 11 and 8 mg O$_2$ dm$^{-3}$, and the decrease in the O$_2$ concentration during the incubation was 2–20%. Neither the initial concentration nor the percentage decrease of O$_2$ concentration during incubation affected the O$_2$ consumption rate. The respiratory quotient (RQ) of 0.85 (e.g. Wetzel 2001) was used to convert O$_2$ consumption to CO$_2$ production.

The benthic respiration from 1 January to 6 May and 11–31 December 1980 (winter respiration) was estimated using a temperature–oxygen consumption regression equation (paper II), and by utilizing unpublished temperature data for Storfjärd from the Finnish Institute of Marine Research, Helsinki (from 2009: Marine Research Centre, Finnish Environment Institute SYKE, Helsinki). Annual respiration was obtained by summing up winter respiration and integrated O$_2$ consumption values that were measured during the study.

The respiration of the benthic amphipod Monoporeia affinis (in paper II referred to as Pontoporeia affinis), a dominant macrofaunal species in the area, was calculated by converting the length of each Monoporeia affinis individual in the cores to body mass (ash-free dry weight (AFDW)), using regressions of Uitto (A. Uitto unpubl. data) and subsequently developing a predictive regression for the dependence of respiration on body mass and temperature, as described in paper II. The respiration of meio- and macrofauna was estimated from the abundance data of Keynäs and Keynäs (1978), derived from Tvärminne Storfjärd in 1977, using body mass (AFDW) values and production to body mass and respiration to production ratios from own observations and from the literature, as described in paper II.

The water temperature over the sediment surface was measured in connection with sediment sampling. Chlorophyll-a values from April to June 1980 were obtained from Hällfors et al. (1983); from July onwards, chlorophyll-a was measured with the same method (spectrophotometric measurements of absorbance at 663 nm after extraction in methanol) in paper II.

2.4 Mesocosm experiments for CH$_4$ emission and oxidation — Lake Pääjärvi

In a mesocosm study of littoral CH$_4$ fluxes, three experimental and three control mesocosms with two bottom types, silt and sand, were established for CH$_4$ emission and oxidation measurements. They were situated on an open meadow close to Lake Pääjärvi (Fig. 1; paper III). Rhizomes of E. fluviatile, originating from the littoral zone of Lake Pääjärvi, were planted into polypropene plastic buckets (height 0.4 m, surface area 0.086 m$^2$, volume 0.03 m$^3$) on organic silt sediment from the lake littoral or sand (grain size 0.1–1 mm) from an esker from the catchment area of Lake Pääjärvi. The buckets were kept filled with water from Lake Pääjärvi so that the water level was always at least 5 cm above the sediment surface.

The gas exchange between air and vegetation/water interfaces was measured with a closed-chamber technique (paper III). The rates of CH$_4$ emission and net ecosystem exchange of CO$_2$ (NEE) in the mesocosms were
measured once a month from 23 May to 20 September 2000. The change in CH$_4$ concentration in the chamber was measured with a gas chromatograph equipped with a flame ionization detector (FID). Prior to CH$_4$ sampling, NEE was measured as the change in CO$_2$ concentration in the chamber with an infra-red CO$_2$ analyser (LICOR LI-6252). On rainy days CO$_2$ was analysed in the laboratory with an infra-red carbon analyser. The rates of CH$_4$ emission and NEE were calculated from the slope of the linear regression between the headspace gas concentration and the incubation time. The net CH$_4$ emission estimates for the whole growing season were made by areal integration of emission values measured in light and oxic environment. Due to the diffuse mode of ventilation by *E. fluviatile* (Hyvönen et al. 1998), no correction for diel CH$_4$ emission variation was made. For more details of the equipment and the methods, see paper III.

CH$_4$ oxidation was estimated by the light-oxic/dark-anoxic (LO/DA) technique (e.g. Lombardi et al. 1997, van der Nat and Middelburg 1998b). CH$_4$ emission rates from both experimental and control mesocosms were first measured in light and oxic (LO) conditions as described previously. Thereafter the experimental mesocosms were incubated for 12–16 h in anoxic N$_2$ atmosphere using darkened incubation chambers (dark-anoxic incubation, DA). Both experimental and control mesocosms were then measured again for NEE and CH$_4$ emission rates (DA measurements; but note that the control mesocosms had not been flushed with N$_2$). To eliminate possible diurnal variation in LO emissions, adjusted LO values for the experimental mesocosms were calculated as follows: the mean difference between DA and LO emissions in the control mesocosms, measured simultaneously during DA and LO measurements in the experimental mesocosms, was added to the LO values of the experimental mesocosms (paper III). The difference between DA and adjusted LO emission rates in experimental mesocosms was considered to represent the amount of methanotrophic activity in the sediment. For statistical analyses of net CH$_4$ emission data the LO values from treated (experimental) mesocosms and all CH$_4$ emission values from controls were combined. DA values of experimental mesocosms were regarded as potential emission of CH$_4$ and were treated separately.

The number of *E. fluviatile* shoots was counted and their total length was measured from each mesocosm after each CH$_4$ emission and oxidation measurement. For biomass estimates, randomly chosen shoots from both bottom types were cut on 27 July. The length–dry weight regression equations (paper III) obtained separately for both bottom types were applied for shoot weight estimation during the whole growing season. After the last LO/DA treatment and gas flux measurements in September, the rhizome biomass was determined for each mesocosm.

Solar radiation and air temperature were recorded continuously at 10 min intervals. Sediment temperature was measured continuously in one mesocosm with organic sediment at a depth of 20 cm below the sediment surface. During the measurements of CH$_4$ emissions and NEE the air temperature in the chambers was measured. WM, water content, DM and OM of the sediments were determined for each mesocosm at the end of the experiment. For details, see paper III.

2.5 CH$_4$ fluxes in vegetated lake littoral — Lake Ekojärvi

Spatial variation of CH$_4$ efflux from the littoral zone of Lake Ekojärvi was studied with a closed-chamber technique for three summer days in 22 vegetation stands, consisting of three emergent and three floating-leaved species, *P. australis, E. fluviatile, Schoenoplectus lacustris, Nuphar lutea, Sparganium gramineum* and *Potamogeton natans*. Littoral CH$_4$ efflux was studied with a closed-chamber technique on 17–19 July 2001, between 9:30 and 15:30 hours each day. The transparent chamber was hung over the shoots of emergent plants with the bottom edge adjusted below the water surface and the accumulation of CH$_4$ in the headspace of the chamber was followed up to 9 min. The CH$_4$ samples were analysed in the laboratory with a
gas chromatograph equipped with FID. For net ecosystem exchange of CO$_2$ (NEE), gas from the chamber was pumped to an LI-6252 CO$_2$ analyser and the changes in CO$_2$ concentration and temperature inside the chamber, and solar radiation (PAR 400–700 nm) outside the chamber (LI-1905A 211 quantum sensor connected to LI-1400 data logger) were recorded up to 3 min. Among the stands of floating-leaved vegetation, only CH$_4$ fluxes were measured. The measurements for the accumulation of CH$_4$ (up to 6 min) were conducted and temperature inside the chamber was recorded. NEE rate was calculated as a linear decrease in CO$_2$, and CH$_4$ emission as a linear increase in CH$_4$ over time.

After the gas sampling, the number of shoots (emergent plants) or leaves (floating-leaved) in the chamber was counted. For biomass determinations, the shoots of the emergent plants were cut just above the sediment surface and the emerged and submerged parts were separated. For the floating-leaved plants, only the shoots with leaves rising above the surface level were taken. Water depth at each study site was recorded and the water temperature was measured at 0.2 m depth and above the sediment surface with a portable dissolved oxygen and temperature meter kit. Data for weather variables were obtained from an automatic weather station 14 km south of Lake Ekojärvi (Potato Research Institute, Lammi, Finland).

For additional information on the stands of floating-leaved vegetation, the percentage cover of the studied stands was estimated. Sediment samples from the emission study sites were taken with steel corers from the uppermost 30-cm sediment layer, where the bulk of the roots and rhizomes exist, and water content, dry mass (DM) and loss on ignition (LOI) of the sediment were determined from sub-samples excluding roots and rhizomes. The exposure of the vegetation stands to waves was assessed by calculating the MF in five directions from the shoreline. Principal component analysis (PCA) was used to summarize and visualize the major patterns of variation in CH$_4$ emissions and other differences between the vegetation stands. Other variables were shoot/leaf density, biomass of plants above the water surface, mean shoot/leaf weight, sediment LOI, water depth and mean fetch (MF). The mean values for each stand were used in the analysis, and all data were log-transformed prior to analysis. All methods are described in detail in paper IV.

2.6 Regional CH$_4$ efflux in vegetated littoral

For regional CH$_4$ emission estimates for vegetated lake littoral (paper V), the coverage of littoral vegetation in all lakes of the study region (Regional study area; Fig 1.) was estimated using the plant coverage data obtained from Vegetation Study Lakes (VegSL). Coverages of littoral vegetation were estimated for both the total lake area in the study region and separately for the lake size classes of 0.001–0.01, 0.01–0.1, 0.1–1, 1–10 and 10–50 km$^2$.

To obtain regional estimates for total and emergent macrophyte vegetation of lake littorals, the VegSL data was used to construct regression models that related the total and emergent macrophyte coverage to the lake area or the shoreline length. For coverage estimates of individual zone-forming emergent species, the lake area–total emergent macrophyte coverage regression models (paper V: table 3) were used together with VegSL mapping data of emergent species coverage.

Regional CH$_4$ effluxes were estimated for two emergent and four floating-leaved species. The species were the emergents *P. australis*, *E. fluviatile* and the floating-leaved *N. lutea*, *P. natans* and *Sparganium* spp. (*S. gramineum* and *Sparganium emersum*). The growing season emissions of CH$_4$ for the species were obtained either directly or by recalculating from published data on four lakes in the Regional study area, lakes Pääjärvi, Alinen Rautjärvi, Ekojärvi and Vesijärvi (for data used, see paper V: table 2).

To demonstrate the inter-annual, temperature-dependent variation of regional CH$_4$ emissions from the vegetated littorals, the total regional emissions were estimated for the two dominant emergent macrophyte species, *P. australis* and *E. fluviatile* for five growing seasons 1998–2002 (for temperature characteristics of
different years, see paper V: table 1). To calculate the emissions, the species-specific air temperature–CH$_4$ emission regression models were used (paper V). The $P$. australis model was derived from the relationship between air temperature and CH$_4$ emission in shallow (10–20 cm water depth) $P$. australis littoral of Lake Vesijärvi (data from Kankaala et al. 2004). The E. fluviatile model was calculated using the data from the E. fluviatile stand of Lake Pääjärvi (Hyvönen et al. 1998, paper III).

The regional estimates for the emissions from $P$. australis and E. fluviatile stands during the growing seasons 1998–2002 were calculated separately for each day using the species-specific temperature response models, the daily mean temperatures during growing season of the appropriate year and the total coverage of the species in the lakes of the region (paper V).

To compare the littoral CH$_4$ emissions and emissions from natural open peatlands on the same region, the total area of natural open peatland (natural minerogenous fens and ombrogenous bogs) in the Regional study area was estimated by combining the data from the European CORINE2000 Land Cover database (Finnish Environment Institute SYKE) and the Topographic Database of Finland (the National Land Survey of Finland) (paper V). The regional CH$_4$ emissions were estimated using the emission data of Nykänen et al. (1998), obtained from natural open ombrogenous bog and minerogenous fen sites in the southern and middle boreal zones in Finland. The two-year average areal CH$_4$ fluxes (15 May–15 September) of the peatland sites were 6 g C m$^{-2}$ yr$^{-1}$ and 14 g C m$^{-2}$ yr$^{-1}$, respectively.

### 3 Main results

#### 3.1 Benthic CO$_2$ production in Lake Pääjärvi and the brackish water site Tvärminne, Storfjärd

##### 3.1.1 CO$_2$ production rates

CO$_2$ production rate from the sediment varied by up to two orders of magnitude in Lake Pääjärvi (Table 3; paper I), the range of CO$_2$ production rate being 0.1–79 mg C m$^{-2}$ h$^{-1}$. The highest values were obtained in laboratory studies when temperature was increased to 30 ºC, and the lowest in the field in winter at 0.5 ºC.

Sediment CO$_2$ production rate in field incubations in Ronninlahti Bay of Lake Pääjärvi varied with water depth and season (Table 3; Paper I: fig. 3). In summer the production rates of the shallow 1.2 and 2.5 m littoral sediments were about nine times higher than those of the 40 m profundal, being 10 and 9 vs. 1 mg C m$^{-2}$ h$^{-1}$, respectively. The seasonal differences were also greatest in shallow water: at 1.2 and 2.5 m, the summer CO$_2$ production rates were 83- and 15-fold compared to those in winter, respectively. In laboratory incubations, using the sediment material from Pappilanlahti Bay, the CO$_2$ production from the sediment also varied with sampling season and water depth (Table 3; paper I).

From spring to autumn, zones with rather homogenous seasonal CO$_2$ production could be distinguished in the lake bottom: e.g. in spring, 2.5–5 and 10–40 m zones had similar CO$_2$ production (log-transformation; ANOVA; Tukey’s HSD test, P≤0.05). In winter, the shallowest site (1.2 m) had the lowest sediment CO$_2$ production rate, 0.1 mg C m$^{-2}$ h$^{-1}$ (Table 3; paper I: fig. 3). At the other depths, winter CO$_2$ production rate was virtually uniform except for the somewhat lower production at 10 m. At 20 and 40 m, mean CO$_2$ production rate did not show significant variation by depth or season. Only in summer was CO$_2$ production at 20 m slightly higher than in the other seasons.

In the absence of continuous temperature records in the water overlying the sediment, the annual CO$_2$ output from Lake Pääjärvi sediment was estimated by integrating the seasonal CO$_2$ production from Ronninlahti Bay field measurements across the depth zones of the lake (Fig. 2; paper I: table 2). This approach may yield the most realistic estimate available, because the general characteristics of the sites used for field observations are probably representative of the main basin of Lake Pääjärvi.

The calculated mean annual area-weighted CO$_2$ production of the sediment of Lake Pääjärvi was 17 g C m$^{-2}$ yr$^{-1}$, and the total an-
Table 3. Carbon gas fluxes from sediments and temperature regime during flux measurements. Fluxes are calculated from data in papers I–IV and all data is converted to carbon units. lab = laboratory incubation; field = field incubation.

<table>
<thead>
<tr>
<th>Gas flux and study site</th>
<th>Water depth (m)</th>
<th>Carbon gas flux (mg C m(^{-2}) h(^{-1}))</th>
<th>Temperature (°C)</th>
<th>Ref.</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Min</td>
<td>SD</td>
<td>n</td>
<td>Max</td>
</tr>
<tr>
<td><strong>CO(_2) production</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lake Pääjärvi, Pappilanlahti Bay, <em>Equisetum fluviatile</em> zone, early summer (lab)</td>
<td>0.4</td>
<td>3.7</td>
<td>2</td>
<td>30.7</td>
</tr>
<tr>
<td>Lake Pääjärvi, Pappilanlahti Bay, <em>Equisetum fluviatile</em> zone, late summer (lab)</td>
<td>0.4</td>
<td>8.1</td>
<td>3.7</td>
<td>79.1</td>
</tr>
<tr>
<td>Lake Pääjärvi, Pappilanlahti Bay, profundal, winter (lab)</td>
<td>5</td>
<td>0.9</td>
<td>0.1</td>
<td>6</td>
</tr>
<tr>
<td>Lake Pääjärvi, Ronnilahti Bay, all seasons (field)</td>
<td>1.2</td>
<td>0.1</td>
<td>2</td>
<td>10.5</td>
</tr>
<tr>
<td>“</td>
<td>2.5</td>
<td>0.6</td>
<td>0.1</td>
<td>5</td>
</tr>
<tr>
<td>“</td>
<td>5</td>
<td>0.5</td>
<td>0.1</td>
<td>5</td>
</tr>
<tr>
<td>“</td>
<td>10</td>
<td>0.3</td>
<td>0.2</td>
<td>5</td>
</tr>
<tr>
<td>“</td>
<td>20</td>
<td>0.4</td>
<td>0.1</td>
<td>5</td>
</tr>
<tr>
<td>“</td>
<td>40</td>
<td>0.6</td>
<td>0.2</td>
<td>4</td>
</tr>
<tr>
<td>Gulf of Finland, Tvärminne, Storfjärd, soft bottom (lab)*</td>
<td>26</td>
<td>1.7</td>
<td>–</td>
<td>12.0</td>
</tr>
<tr>
<td><strong>Net CH(_4) emission</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lake Pääjärvi, mesocosm, <em>Equisetum fluviatile</em>, organic sediment</td>
<td>~0.05</td>
<td>2.6</td>
<td>0.3</td>
<td>3</td>
</tr>
<tr>
<td>Lake Pääjärvi, mesocosm, <em>Equisetum fluviatile</em>, sand</td>
<td>~0.05</td>
<td>0.0</td>
<td>0.0</td>
<td>3</td>
</tr>
<tr>
<td>Lake Ekojärvi, Phragmites australis stand, lake littoral</td>
<td>0.4–0.6</td>
<td>–</td>
<td>–</td>
<td>3</td>
</tr>
<tr>
<td>Lake Ekojärvi, Schoenoplectus lacustris, lake littoral</td>
<td>0.5–0.9</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Lake Ekojärvi, <em>Equisetum fluviatile</em>, lake littoral</td>
<td>0.6–1.0</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Lake Ekojärvi, <em>Nuphar lutea</em>, lake littoral</td>
<td>0.6–1.0</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Lake Ekojärvi, Sparganium gramineum, lake littoral</td>
<td>0.4–0.6</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Lake Ekojärvi, <em>Potamogeton natans</em>, lake littoral</td>
<td>0.6–1.0</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td><strong>Potential CH(_4) emission</strong></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lake Pääjärvi, mesocosm, <em>Equisetum fluviatile</em>, organic sediment</td>
<td>~0.05</td>
<td>3.8</td>
<td>–</td>
<td>3</td>
</tr>
<tr>
<td>Lake Pääjärvi, mesocosm, <em>Equisetum fluviatile</em>, sand</td>
<td>~0.05</td>
<td>0.2</td>
<td>–</td>
<td>3</td>
</tr>
<tr>
<td><strong>CH(_4) oxidation</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lake Pääjärvi, mesocosm, <em>Equisetum fluviatile</em>, organic sediment</td>
<td>~0.05</td>
<td>1.7</td>
<td>0.1</td>
<td>3</td>
</tr>
<tr>
<td>Lake Pääjärvi, mesocosm, <em>Equisetum fluviatile</em>, esker sand</td>
<td>~0.05</td>
<td>0</td>
<td>–</td>
<td>3</td>
</tr>
</tbody>
</table>

* Estimated from O\(_2\) consumption, RQ = 0.85 (Wetzel 2001)
Annual production for the whole lake was 2.3 x 10^5 kg C yr^{-1}. The majority of the annual CO2 production (c. 70%) occurred during summer and >80% was produced during the spring and summer months. The contributions of autumn and winter were both less than 10%. About 30% (4 km^2) of the bottom sediment area of Lake Pääjärvi lies at a water depth of 0–3 m, and 9% (0.36 km^2) of this is covered by emergent or floating-leaved flora (calculated from S. Mäkelä, unpubl. data). According to Ruuhijärvi (1974) and Kansanen and Niemi (1974), the lower limit of macrophytes in Lake Pääjärvi is around 1.5 m, owing to the relatively high water colour, 40–60 mg Pt L^{-1}. In terms of annual benthic CO2 production, however, the role of littoral was remarkable: 53% of the annual production occurred at a depth of 0–3 m. On the whole, the zone approximately equivalent to summer epilimnion (0–10 m) accounted for c. 75% of the estimated annual and for 81% of the summer-time CO2 production. Sediments deeper than 15 m water depth accounted for only 16% of the annual CO2 production, despite making up 33% of the lake bed.

Daily O2 consumption of sediment in the brackish water site, Tvärminne Storfjärd (Fig. 1), varied between 0.13 and 0.90 (median 0.35, mean 0.41) g O2 m^{-2} d^{-1} (paper II). This corresponds, using RQ = 0.85, to a CO2 production of 1.7–12 mg C m^{-2} h^{-1} (Table 3). The cumulative oxygen consumption for the period May to December was 82 g O2 m^{-2} (26 g C m^{-2}). Two maxima were observed in the total benthic respiration during the study period (paper II). The highest value was found in mid-July, but an almost equally high value was encountered in early May. In addition, there was a lower peak in late autumn. Annual benthic respiration was 111 g O2 m^{-2} yr^{-1} or, assuming RQ = 0.85, 35 g C m^{-2} yr^{-1}.

Input of the organic matter from the overlying water mass to the sediment was not directly measured but the chlorophyll-a values of the water column (paper II) provide an indirect measure of fresh biomass available for sedimentation. In the study area, as in the whole northern Baltic Sea, a major part of the annual sedimentation is coupled with the spring peak of phytoplankton (e.g. Kuparinen et al. 1984). The phytoplankton chlorophyll-a values at Storfjärd in 1980 showed a high maximum in early spring (mid-April to early May) (Hällfors et al. 1983) and consistently lower values with minor variations during the rest of the year (paper II: fig. 1). The high benthic res-
piration found on the first study date coincided with the last phases of the vernal phytoplankton maximum. Only a small peak in chlorophyll-\(a\) values was observed during the high summer maximum of benthic respiration. This could be connected with a temporary accumulation at Storfjärd of a thick layer of warm surface water rich in phytoplankton (cf. Niemi 1975).

The annual respiration of \(M.\) affinis was 34.7 g O\(\text{2}\) m\(-2\) yr\(^{-1}\) (11 g C m\(^{-2}\) yr\(^{-1}\)), or about 31% of the total annual benthic respiration. The annual respiration of \(M.\) affinis calculated from the data of Keynäs and Keynäs (1978) was 12 g C m\(^{-2}\) yr\(^{-1}\), and from the production data of Uitto (Uitto A., unpublished) 11.6 g C m\(^{-2}\) yr\(^{-1}\).

The summed respiration of the whole meio- and macrofauna, estimated from the abundance data of Keynäs and Keynäs (1978), was 23.7 g C m\(^{-2}\) yr\(^{-1}\) or 67% of the total benthic respiration.

### 3.1.2 Effects of temperature and other factors

A strong exponential relationship (\(r^2 = 0.90\)) of sediment CO\(_2\) production with sediment temperature was found in the laboratory studies on littoral and profundal sediments of Pappilanlahti Bay, the western bay of Lake Päijärvi (Fig. 3a, equations 1, 2, 4; paper I: table 1, equations 1–3). The response of CO\(_2\) production to a change in temperature was statistically similar at each sampling date and site (ANCOVA). With a 10 °C change in temperature, the CO\(_2\) production rate changed by a factor of 2.7 (also referred to as temperature sensitivity or \(Q_{10}\) value). However, between different sites and seasons there was high variation in temperature-adjusted CO\(_2\) production rate which could be seen in different intercepts of the equations. At the same laboratory temperature, the CO\(_2\) production rate of the littoral (water depth 0.4 m) sediment in late summer was twice as high as in early summer and seven times higher than the rate in low profundal (water depth 5 m) sediment in winter.

In the field study in Ronninlahti Bay of Lake Päijärvi, the temperature of water overlying the sediment varied between 0.5 and 15.7 °C (paper I). In winter, the temperature varied from 0.5 °C (2.5 m depth) to 1.6 °C (40 m depth) and in summer (July) from 5.4 °C (40 m depth) to 15.7 °C (5 m depth). In summer the epilimnion was c. 10 m deep. Below the lower boundary of metalimnion at 20 m, the temperature never exceeded 6.6 °C.

Temperature was also a key factor affecting sediment CO\(_2\) production in Ronninlahti Bay. The exponential model which was found to describe best the temperature dependence in Pappilanlahti Bay in laboratory experiments, was used also here. Most of the seasonal variation in CO\(_2\) production (70–94%) could be explained by temperature at each depth zone, except at 40 m where temperature remained almost constant throughout the year (Fig. 3b, equations 1–3; paper I: table 1, equations 4–9).

The slope parameters (describing the dependence of the CO\(_2\) production rate on temperature) of the regression models for 2.5 and 5 m were identical, but the basic production rates (intercepts) differed, whereas common slope and intercept values were applicable in the temperature dependence models for the depths of 1.2, 10 and 20 m (paper I). The temperature response of CO\(_2\) production was smaller at 2.5 and 5 m than at the three other depths, but the basic production rate was higher. This resulted in higher production rates at 2.5 and 5 m at temperatures of < 15.4 and 8.8 °C, respectively (Fig. 3b). With a 10 °C change in temperature, the CO\(_2\) production in the field measurements rate changed by a factor of 10.3 at the depths of 1.2, 10 and 20 m, and by 5.2 at depths of 2.5 and 5 m.

Temperature explained 69 and 79% of the variation in sediment CO\(_2\) production over the whole depth gradient in Ronninlahti Bay in spring and summer (paper I: table 1, eqns 11 and 12). However, sediment dry mass (DM) alone was a somewhat better predictor, explaining 72 and 83% of the variation, respectively. Both temperature of the water overlying the sediment and DM correlated closely with each other and with water depth (Pearson correlation; \(P \leq 0.05\)).

The temperature dependence of the sediment CO\(_2\) production at all depths in Ronninlahti Bay was considerably stronger than in Pappilanlahti Bay (paper I: table 1). However, because of
Figure 3. Effect of temperature on carbon gas fluxes in lake and brackish water sediments. a. CO₂ production in Lake Pääjärvi, Pappilanlahti Bay (laboratory study; paper I) and lakes Vallentunasjön and Svarttjärn, Sweden (data from Gudasz et al. 2010) b. CO₂ production in Lake Pääjärvi, Ronninlahti Bay (field study; paper I) and Tvärminne, Storfjärd (laboratory study; paper II). 'a' denotes that the value does not differ from zero. (t-test, P<0.001). c. CH₄ emission in Lake Pääjärvi (mesocosm study; paper III), Lake Pääjärvi, Pappilanlahti Bay (field study; ref. Hyvönen et al. 1998 in paper III) and Lake Vesijärvi (field study; data from Kankaala et al. 2004 in paper V). Equations: X = temperature in water overlying sediment°C; Y = carbon gas flux (mg C m⁻² h⁻¹). Efluv = Equisetum fluviatile stand, Phaus = Phragmites australis stand, O = organic sediment, S = sand, P = potential emission, N = net emission. Note the different scales in the figures.

1 Originally measured as O₂ consumption, respiratory quotient RQ = 0.85 (Wetzel 2001).
2 Fig 3c, eqn (2) and (4): X = air temperature.
the lower basic level (intercept) of the regression models in Ronninlahti Bay, the predicted \( \text{CO}_2 \) production rates at a given depth and temperature did not always exceed those in Pappilanlahti Bay. For example, at a depth of 5 m, the temperature–\( \text{CO}_2 \) production model of Ronninlahti Bay sediment indicated about 2.3 times greater temperature dependence than that of Pappilanlahti Bay at 5 m (paper I: table 1, eqns 1 and 6), although at temperatures below 9 °C the predicted \( \text{CO}_2 \) production rates were lower in Ronninlahti Bay.

The properties (WM, DM, MM and OM and the relative proportions of DM of WM and OM of DM) of the upper 2 cm of the sediment in Ronninlahti Bay varied with depth and season (paper I: fig. 2). In the littoral zone, especially at 1.2 m, OM% was very low. This was evidently because of the erosion of the rather open littoral. The seasonal changes in sediment properties were particularly remarkable at the 1.2, 2.5 and 5 m sampling sites. For example, for the mean concentration of OM at a given depth, the coefficient of variation (CV) between the seasons at these depths was 17–43%, whereas in the 20 and 40 m sediments it was 3–5%. The spring values of all sediment properties at 1.2 m differed remarkably from other seasons and depths.

The sediment properties (except OM) correlated with water depth or temperature (Pearson correlation \( P \leq 0.05 \)). In water shallower than 20 m, distinct seasonal changes in the sediment properties were observed from winter to summer along the depth gradient (ANOVA; Tukey’s HSD test, \( P \leq 0.05 \)). At 20 and 40 m depth, variation was negligible throughout the year.

The near-bottom temperature during the study period in Tvärminne, Storfjärd was usually less than 10 °C. The variation of total respiration values also appeared generally to follow the variation of temperature here, with the exception of the first study date, 7 May when the last phases of vernal phytoplankton maximum coincided with the high respiration value, although temperature was still low (paper II: fig. 1). In a linear regression equation about half of the variation of total benthic respiration (calculated from the medians of replicate respiration measurements and excluding the first study date) could be explained by the temperature (paper II). The regression equation in which the parameters were transformed to give \( C \) values for respiration is given in Fig. 3b, eqn 4 (\( C \)-values calculated from oxygen consumption data in paper II. \( R^2 = 0.85 \)).

The respiration of \( M. \) affinis explained generally 20–40% of the total respiration, although higher percentages were occasionally found (paper II). The percentage contribution of \( M. \) affinis, calculated from simultaneous, independent population estimates (Uitto A., unpublished), was also about 30%.

3.2 \( \text{CH}_4 \) flux from littoral sediments in lakes Pääjärvi and Ekojärvi

3.2.1 Littoral \( \text{CH}_4 \) emission and \( \text{CH}_4 \) oxidation

Net \( \text{CH}_4 \) efflux of the littoral zone of lakes Pääjärvi (mesocosm study) and Ekojärvi varied between 0 and 14 mg C m\(^{-2}\) h\(^{-1}\) (Table 3). In Lake Pääjärvi littoral, the net emission rate of \( \text{CH}_4 \) (mean ± SE) from the \( E. \) fluviatile stands growing on the organic sediment was 5.8 ± 0.4 mg C m\(^{-2}\) h\(^{-1}\) in May, increasing to 14.3 ± 0.6 and 13.2 ± 0.4 mg C m\(^{-2}\) h\(^{-1}\) in June and July, and decreasing again to 2.6 ± 0.2 mg C m\(^{-2}\) h\(^{-1}\) towards September (paper III: fig. 2a). The net emission rates from the \( E. \) fluviatile stands growing on sand bottoms (paper III: fig. 2b) were very low, about 3–10% of those measured simultaneously from the organic sediment. The highest emissions, 0.8–1.3 mg C m\(^{-2}\) h\(^{-1}\), were measured in July and August. No net \( \text{CH}_4 \) emission was detected in two sand mesocosms in May and in four mesocosms in September.

Potential \( \text{CH}_4 \) emission rates in Lake Pääjärvi mesocosms varied during the study period between 3.8 and 24.2 mg C m\(^{-2}\) h\(^{-1}\) in the organic sediment and between 0.2 and 1.4 mg C m\(^{-2}\) h\(^{-1}\) in the sandy bottom (Table 3; paper III).

Oxidation of \( \text{CH}_4 \) was detected throughout the growing season in all \( E. \) fluviatile stands growing on the organic sediment (paper III). The highest \( \text{CH}_4 \) oxidation rates were measured in June and July, 8.8 and 10.8 mg C m\(^{-2}\) h\(^{-1}\),
respectively (Table 3; paper III). The highest percentages of CH$_4$ oxidized were in May and September (51.8% and 46.1%) and the lowest in August (26.9%), but the differences between months were not statistically significant. In E. fluviatile stands growing on sand the oxidation of CH$_4$ varied between 0 and 0.6 mg C m$^{-2}$ h$^{-1}$ (Table 3). In May no estimates of oxidation were made. From June to August ca. 40% of the potential CH$_4$ emission was oxidized, but no oxidation was detected in September.

The total net emission of CH$_4$ during the study period (23 May – 19 September) was 27.6 ± 0.6 (SE) g C m$^{-2}$ from the organic bottom and 2.0 ± 0.3 g C m$^{-2}$ from sand. Related to the maximum shoot biomass during the growing season, the CH$_4$ emission expressed as carbon was significantly higher from the organic sediment (6.5 ± 0.4%) than from sand (1.7 ± 0.3%) mesocosms (t = 8.672, p < 0.001, df = 10) (paper III).

3.2.2 CH$_4$ flux, temperature and sediment quality

In Lake Pääjärvi mesocosms, the variation in net CH$_4$ emission rates in the organic sediment significantly correlated (p < 0.001) with sediment temperature (Fig. 3c, eqn 3; paper III: table 2). The relationship was best described with an exponential model, which explained 92% of the observed variation. All other factors that were studied had much smaller ($r^2$ = 0.3–0.09), although statistically significant, effects on net emission rates (negative correlation: shoot biomass, NEE, instantaneous irradiation; positive correlation: monthly sum of irradiation).

When plotted against air temperature, the daily means of net CH$_4$ emission from organic sediment mesocosms were close to the values measured from the littoral of Lake Pääjärvi from June to September 1994 and 1995 (emission data from Hyvönen et al. 1998) (Fig. 3c, eqn 2; paper III: fig. 3). The air temperature–net CH$_4$ emission exponential models explained 90.1% of the variation for organic sediment mesocosms and 82.3% of the variation for the littoral of Lake Pääjärvi, respectively. The slopes of the two regression equations did not differ significantly (paper III). In sand mesocosms 62.6% of the observed variation in net emission was explained by the variation of shoot biomass of E. fluviatile. There was also a very significant linear correlation between net emission and sediment temperature ($r^2$ = 0.52; Fig. 3c, eqn 6). However, due to the significant correlation between shoot biomass and sediment temperature, sediment temperature was not included as an additional independent variable in a multiple regression model together with shoot biomass (paper III). There was also a slight but significant negative correlation between net CH$_4$ emission and instantaneous irradiation in sand mesocosms.

On both bottom types, organic sediment and sand, potential CH$_4$ emission was also significantly correlated with the daily mean of sediment temperature and was best described with exponential models (Fig. 3c, eqns 1 and 5; paper III: table 3). The slopes of the regression equations did not differ significantly, but the difference in intercepts was statistically significant. Temperature sensitivity ($Q_{10}$) values calculated from the exponential models were 4.9 and 5.6 for net and potential CH$_4$ emission in the organic sediment mesocosms, respectively. The $Q_{10}$ value for potential CH$_4$ emission in sand mesocosms was 4.4. In sand mesocosms potential CH$_4$ emission was also significantly correlated with shoot biomass and there was intercorrelation with sediment temperature; thus its influence could not be treated separately.

CH$_4$ oxidation rate did not correlate with temperature, and the percentage of CH$_4$ oxidized did not statistically differ between months, although the highest values were in May and September (8.5 and 10.8 mg C m$^{-2}$ h$^{-1}$, respectively).

In Lake Ekojärvi, the mean CH$_4$ efflux from 22 emergent and floating-leaved vegetation stands ranged between 0.8 and 20 mg C m$^{-2}$ h$^{-1}$ (Table 3; paper IV: fig. 4). The highest emissions were from the emergent P. australis stands, being 6–20 mg C m$^{-2}$ h$^{-1}$, followed by S. lacustris > E. fluviatile > N. lutea > S. gramineum > P. natans (ANOVA). Flux from P. australis stands was an order of magnitude higher than that from the other stands. Within-
species differences between stands were not significant. The mean air temperature during gas flux measurements was quite high, 23.4, 22.5 and 21.8 °C for the first, second and third day, respectively, and the water temperature in the studied vegetation stands at 0.2 m from the bottom also varied between 21.3 and 22.9 °C (paper IV). The variation was so small that temperature could be considered as constant during the experiment.

Throughout the study period, the primary productivity exceeded the community respiration rate in Lake Ekojärvi. In the stands of *P. australis*, net primary productivity (NPP) varied between 10 and 109 mg C m$^{-2}$ h$^{-1}$ (paper IV). NPP was related to the maximum rate of productivity and solar radiation. In the stands of *S. lacustris* and *E. fluviatile*, NPP was of the same order of magnitude as measured in *P. australis* stands, but it was less clearly related to solar radiation. In the emergent vegetation stands studied, NPP correlated with neither the density nor the biomass of shoots.

### 3.2.3 CH$_4$ emission, plant species and other environmental variables — Lake Ekojärvi

In Lake Ekojärvi, the effects of littoral plant species and environmental variables other than temperature on CH$_4$ emission were also studied. The short measurement period in similar weather conditions ensured that the often dominating effect of spatial and temporal variation of temperature (maximum difference above sediment surface 1.6 °C) on the results was negligible and could be ignored.

When the CH$_4$ emissions were related to environmental variables (shoot/leaf density, biomass of plants above the water surface, mean shoot/leaf weight, sediment LOI, water depth and mean fetch (MF)), four groups of vegetation could be distinguished along the PCA ordination (paper IV: fig. 5). The first group was formed by *P. australis* stands, showing high CH$_4$ emission (mean 6–20 mg C m$^{-2}$ h$^{-1}$) and high biomass per plant shoot and per unit area. The second group was formed by *E. fluviatile* and *S. lacustris* stands. These grew in dense stands but were more wave-exposed and released CH$_4$ more slowly than *P. australis* stands. The third group was formed by all *N. lutea* stands. They favoured soft organic sediments and released CH$_4$ significantly more slowly than *P. australis* stands. The fourth group, from which CH$_4$ emissions were lowest, consisted of *P. natans* and *S. graminæum* stands.

About 90% of the variation in CH$_4$ emissions in all stands of emergent macrophytes was explained by a multiple regression model in which independent variables were mean dry weight of plant shoots above water surface and MF of the growing site (for equation, see paper IV). In stands of *P. australis*, a linear relationship was found between stand-specific mean values of CH$_4$ emissions and NPP ($r^2 = 0.99$) as well as between the mean CH$_4$ emission and mean solar radiation ($r^2 = 0.96$). Such relationships were not present in *S. lacustris* and *E. fluviatile* stands. The proportion (%) of released CH$_4$ to NPP, in units of carbon, was significantly higher ($P < 0.001$) in *P. australis* stands (mean ± SE, 7.4 ± 0.5%) than in stands of *S. lacustris* and *E. fluviatile* (0.5 ± 0.1% in both).

In stands of *S. graminæum* and *P. natans*, CH$_4$ emissions were not related to any of the measured environmental variables. In *N. lutea* stands, CH$_4$ emission was correlated with the MF of the growing site and the percentage cover of leaves in the vegetation stands. However, there was a significant negative correlation between MF and percentage cover of leaves ($r^2 = 0.90$), and thus the influences of these variables on CH$_4$ emission could not be separated from each other.

The grazing of *N. lutea* leaves by its herbivore *Galerucella nymphaeæ* (Coleoptera, Chrysomelidae), which was abundant on the study sites, did not affect CH$_4$ release (Mann-Whitney U-test). As indicated by PCA, CH$_4$ emissions were significantly correlated with the biomass of the vegetation stands when the data of emergent and floating-leaved vegetation were combined. An exponential model with dry weight of the biomass above the water surface as an independent variable explained 57% of the observed variation in CH$_4$ emission (paper IV).
3.3 Regional CH\textsubscript{4} emissions from vegetated littorals

The proportional coverage of zone-forming emergent and floating-leaved macrophyte species in VegSL lakes varied considerably with lake size (Fig. 4). The five emergent and three floating-leaved species or species groups were considered here. The most extensive stands in relation with total lake area were those of the emergents \textit{P. australis} and \textit{E. fluviatile} and floating-leaved \textit{N. lutea}, 0.9, 1.1 and 1.0%, respectively. The lakes in size class 1–0.1 km\textsuperscript{2} and 0.1–0.01 km\textsuperscript{2} were most extensively vegetated (coverages 18% and 16.5% of total lake area, respectively).

The regional CH\textsubscript{4} emissions of vegetated littorals, and their annual variability, were estimated for littoral \textit{P. australis} and \textit{E. fluviatile} stands of the 1600 km\textsuperscript{2} study region in Häme, southern Finland, during the growing seasons 1998–2002 (Fig. 1). Emissions for \textit{P. australis} stands varied between 6.2x10\textsuperscript{4} (1998) and 8.3x10\textsuperscript{4} (1999) kg C gs\textsuperscript{−1}, and those of \textit{E. fluviatile} between 1.2x10\textsuperscript{5} (1998) and 1.5x10\textsuperscript{5} (1999) kg C gs\textsuperscript{−1} (\textit{paper V}: fig. 5). The role of lakes larger than 1 km\textsuperscript{2} was remarkable when considering the total regional CH\textsubscript{4} emission. The proportional and total coverages of \textit{P. australis} and \textit{E. fluviatile} varied considerably between the lake size classes (Fig. 5; \textit{paper V}: fig. 3). The emissions of the \textit{P. australis} and \textit{E. fluviatile} stands in the lakes larger than 1 km\textsuperscript{2} were 82% and 80% of the total emissions of the respective stands in all lakes in the study region.

The total CH\textsubscript{4} emissions estimated for the zone-forming floating-leaved macrophytes varied considerably between plant species and between the lake size classes, but the variability in plant coverage was even greater (Fig. 5; \textit{paper V}: table 4). In the smallest lake class, 0.01–0.001 km\textsuperscript{2}, \textit{Sparganium} spp. had an areal dominance of 95% of total plant coverage but \textit{P. australis} was the main CH\textsubscript{4} emitter (99% of emissions). \textit{N. lutea} had the greatest total CH\textsubscript{4} emission of the three floating-leaved species or species groups studied here, 3059 kg C during the growing season 2001. This was due to its large total coverage, but it was only 1.4% of the combined emission of \textit{P. australis} and \textit{E. fluviatile}.

![Figure 4](image-url)  
**Figure 4.** Relative coverages of zone-forming emergent and floating-leaved species in the Vegetation Study Lakes (VegSL). Redrawn from \textit{paper V}. 
Figure 5. Relative proportions of coverages of zone-forming emergent and floating-leaved species and their CH$_4$ emissions in different lake size classes in the growing season 2001 in the Regional study area, southern Finland. Data from paper V.
fluvial. *P. natans* and *Sparganium* spp. together had an emission of only half of that of *N. lutea*. Total CH$_4$ emissions of floating-leaved species were negligible compared with the two dominating emergent macrophytes, *P. australis* and *E. fluviatile*.

Air temperature had a pronounced effect on total amounts of CH$_4$ escaping from the *P. australis* and *E. fluviatile* littorals on a regional level (paper V). Daily regional CH$_4$ emissions varied remarkably due to variation of daily mean temperature. On the hottest day of the growing seasons 1998–2002 (1999; daily mean temperature 26.5°C) the daily emissions from the *P. australis* zones in the region were 2.0x10$^3$ kg C d$^{-1}$ and from *E. fluviatile* zones 5.2 x10$^3$ kg C d$^{-1}$. The lowest emissions (1999; daily mean temperature – 4°C) were 58 kg C d$^{-1}$ and 75 kg C d$^{-1}$, respectively. Thus the *P. australis* and *E. fluviatile* stands together produced 53 times more CH$_4$ on the warmest day than on the coolest day of the growing season.

The area of open peatlands in the study region, 13.4 km$^2$, was practically the same as the total area covered by littoral macrophytes, 13.2 km$^2$. The total coverage of *P. australis* and *E. fluviatile* was 5.4 km$^2$, less than half (41%) of the open peatland area. However, the average combined CH$_4$ emission of *P. australis* and *E. fluviatile* littorals (2.2 x10$^3$ kg C gs$^{-1}$) was 1.6-fold compared to the emission of the open peatlands, 1.7x10$^3$ kg C gs$^{-1}$.

### 3.4 Carbon gas flux from the sediment in warming climate

According to model simulations for Lake Pääjärvi (using A2 emission scenario with both ECHAM and HadAM3 general circulation model forcing; Saloranta et al. 2009), median estimates for temperature increase in the 0–1 m water layer for June and August from 1961–1990 to 2071–2100 were 3.13 °C and 2.95°C, respectively. According to temperature–CO$_2$ production models (Fig. 3; paper I: table 1), this increase in temperature would result in a 29% increase in littoral benthic CO$_2$ production in June and a 27% increase in August in *E. fluviatile* stands of Pappilanlahti Bay (paper I). In winter, the corresponding temperature change is 0.23 °C at 5 m depth, which increases CO$_2$ production by 2% in December–January. Similarly, if only the temperature effect is considered, it is also possible to predict the increase in the CH$_4$ emissions in the *E. fluviatile* stands in Lake Pääjärvi using the same temperature scenarios of Saloranta as used in paper I and the temperature–net CH$_4$ emission model estimated for organic bottoms (paper III). The predicted relative increase in littoral benthic CH$_4$ net production in *E. fluviatile* stands for the same time interval of 110 years (1961–1990 and 2071–2100) would be 65% in June and 60% in August. Thus, the relative increase in CH$_4$ net emission would greatly exceed the increase in CO$_2$ emission. Considering that the effect of CH$_4$ on global warming (global warming potential, GWP) is 25-fold higher than that of CO$_2$ for a 100 year time horizon (Forster 2007), the vegetated littorals as producers of CH$_4$ are even more important players in climate warming than earlier assessed.

### 4 Discussion

#### 4.1 Carbon gas flux in aquatic sediments and their controls

##### 4.1.1 CO$_2$ production in Lake Pääjärvi and Tvärminne, Storfjärd

Jones (1980) and Jones and Simon (1981) showed already in the 1980s that there were differences in the abundance and activity of microbtiota in the littoral and profundal areas but that the direction of change varied. In some lakes littoral is more active than profundal sediment (den Heyer and Kalff 1998, paper I), in some others less active (Jones 1980, Jones and Simon 1981, Liikanen et al. 2003a) and sometimes no differences were observed at all (Algesten et al. 2005). Littoral areas also differ from each other in their CO$_2$ production activity, depending on e.g. physical and chemical properties of the bottom and, in vegetated areas, on plant species and coverage (den Heyer and Kalff 1998, paper I).
The CO₂ production rates of Lake Pääjärvi agreed very well with the profundal and both vegetated and unvegetated littoral mineralization rates obtained by den Heyer and Kalff (1998) in unproductive Quebec lakes at corresponding temperatures. They studied the summer sediment metabolism (combined CO₂ and CH₄ production; incubation in dark) using similar sampling and incubation methods to those used in this study and in paper I. Algsten et al. (2005) studied sediment mineralisation activity (combined CO₂ and CH₄ production; incubation in light; hence also negative mineralisation activity values are possible if primary production rate exceeds the mineralisation rate) during summer in unproductive Swedish lakes and measured sediment respiration rates between – 53 and 182 mg C m⁻² d⁻¹ in the mixed layer area, close to the value measured in Lake Pääjärvi, Ronninlahti Bay, 175 mg C m⁻² d⁻¹.

Temperature is one of the major factors affecting the activity of sediment biota (see e.g. the review of Pace and Prairie (2005)). This can also be seen in Lake Pääjärvi, where temperature always explained at least 70%, usually more than 80%, of variation in CO₂ production rates (Figs 3a, 3b; paper I: table 1). Granéli (1978), den Heyer and Kalff (1998), Liikanen et al. (2002, 2003b) and Gudaz et al. (2010) also emphasized the leading role of temperature in controlling sediment mineralisation activity rates. Gudaz et al. (2010) obtained almost exactly the same temperature dependence of organic carbon mineralization in the low profundal sediment of two Swedish lakes as was observed in laboratory experiments on both littoral and low profundal in Lake Pääjärvi, Pappilanlahti Bay (Fig. 3a; paper I: table 1). They also found the same dependence when they analyzed a large dataset gathered by compilation of published data from widely different lakes in different parts of the world.

When relating temperature to seasonal or spatial benthic CO₂ production rates from Lake Pääjärvi, Ronninlahti Bay, the increase of production rate with temperature (the slope of the model equation) was higher and more variable than in the laboratory study of Pappilanlahti Bay, where other variables than temperature were constant (Figs 3a, 3b; paper I: table 1). This may be due to the seasonal and spatial variation in sediment properties in the field. The sediment properties measured here did not correlate well with respiration rates (paper I). In studies on soil organic matter, it has been hypothesized that the decomposition of old and more resistant (low quality) organic matter is more temperature sensitive (higher Q₁₀ value) than that of fresh (high quality) matter (Bosatta and Ågren 1999, Ågren and Wetterstedt 2007, Conant et al. 2008). This could explain the observation that in Ronninlahti Bay the Q₁₀ value of CO₂ production rate was higher at 20 m depth, where the organic matter sedimenting from upper water layers was probably more decomposed and thus of lower quality than at lower depths of 2.5 and 5 m.

Lake Pääjärvi sediment expressed high spatio-temporal heterogeneity in physical and chemical properties (this study, paper I). This variability in turn regulates the quality and quantity of flora, fauna and microbiota in the sediment (Downing and Rath 1988, Ostrovsky et al. 1997, Peeters et al. 2004, Schiefer 2006), and thus also contributes to mineralisation activity, as can be seen in Pappilanlahti Bay (Fig. 3a; paper I). Therefore, all whole lake carbon budgets should include extensive seasonal sampling of both littoral and profundal sediments.

The range and the average level of the daily benthic CO₂ production in brackish water at Tvärminne, Storfjärd were rather similar to those observed by Jansson et al. (1984) and estimated by Gazeau et al. (2004) for European coastal areas. The annual respiration rate was similar to that measured by Wassmann (1984) on the western coast of Norway. The respiration rates in Storfjärd and Lake Pääjärvi, Ronninlahti Bay, were within about the same range (Table 3). This is in accordance with a literature analysis of den Heyer and Kalff (1998), who found that in shallow marine sediments the mineralisation rates were surprisingly similar to those in lakes despite the differences in the environments.

As in lakes, the level of benthic mineralisation in brackish water sediment depends on temperature and also e.g. on the supply of or-
ganic matter, oxygen concentration, sediment resuspension and bioturbation of the sediment by macrofauna (Granéli 1979, Wassmann 1984, Yap 1991, Ståhlberg 2006). On the first study date in Storfjärd, 7 May, chlorophyll-α concentration was still at a high level (paper II) after the spring bloom maximum on 1 May. According to the data of Hällfors et al. (1983) the major part of the bloom sedimented within the first 10 days of May, which probably impacted the respiration that was at a high level although temperature was still low (paper II). After this first date, temperature had the most dominating effect on respiration rate up to December, although it did not explain such a large proportion of variation in respiration rate as in Lake Pääjärvi (Figs 3a, 3b; papers I, II).

Temperature thus appears also to be a major determinant of benthic metabolism in brackish water and in shallow estuary sediments (e.g. van Es 1982, Therkildsen and Lomstein 1993). However, Eriksson Wiklund et al. (2009) noted on the basis of their mesocosm studies that the effects of temperature increase may be more indirect. Temperature may change the food web structure in the northern Baltic Sea towards a less efficient heterotrophic microbial food web, and decrease the pelagic-benthic food web efficiency, leading to decreased transport of lower quality carbon compounds to the benthos. This in turn lowers the benthic productivity, e.g. reproduction success and growth rate of M. affinis which as a stenothermal cold-water species is sensitive to small temperature changes (Eriksson Wiklund and Sundelin 2001, Eriksson Wiklund et al. 2009). A drastic decline of M. affinis has occurred in the Tvärminne region, the species contributing less than 5% of the total zoobenthos abundance in 2000 compared to 90% in the 1920s (Laine et al. 2003). Although the reasons for this decline are obscure (eutrophication is perhaps the most likely factor), the changing interspecific interactions associated with future warming will presumably have further adverse effects on the benthic community.

In Tvärminne Storfjärd, the linear model equation described best the temperature dependence of mineralisation, although in freshwater studies the effects of temperature on both CO₂ and CH₄ fluxes were best expressed by exponential models (Fig. 3; papers I–III). Theoretically, neither linear nor exponential models can describe the respiration over the whole range of temperatures, because they do not take into account the collapse of the biological system if temperature increases too much, or the observation that the temperature sensitivity (Q₁₀) of microbota is probably higher at lower temperatures. These aspects of temperature-heterotrophic respiration models have been considered e.g. by Tuomi et al. (2008) using soil data. However, within the naturally occurring temperatures both linear and exponential models may provide realistic scenarios of the effect of temperature on overall sediment metabolism.

4.1.2 CH₄ flux in lakes Pääjärvi (mesocosm) and Ekojärvi

The net CH₄ emission rates in the mesocosm study of Equisetum fluviatile growing on organic sediment or sand (Table 3) were within the range reported in the literature from vegetated littorals (e.g. Juutinen et al. 2001, Ström et al. 2005, Laanbroek 2010). The total net CH₄ emission (27.6 g C m⁻²) of organic mesocosm (sediment originating from the E. fluviatile littoral of Lake Pääjärvi) during the study period was close to that estimated by Hyvönen et al. (1998) in field experiments performed in the E. fluviatile littoral of Lake Pääjärvi, 32.8 g C m⁻² (paper III). The higher variation of replicate measurements by Hyvönen et al. (1998) was probably due to the greater variability in sediment quality in the field.

The oxidation of CH₄ was estimated with the LO/DA technique, assuming that oxygen depletion does not affect the methanogenesis but stops the oxidation after 12–16 h anoxic treatment. Some authors have observed a stimulation of methanogenesis under prolonged anoxic treatment (Gerard and Chanton 1993, van der Gon and Neue 1996), but in their greenhouse experiments the plants may have suffered from prolonged anoxia (1–7 days) or they were cut above the water level, which probably affected CH₄ production. In the experiments of this study
the plants did not suffer from the night-time N\textsubscript{2} treatment, and the results can be expected to be realistic. This was also evident from the fact that LO (light–oxic) CH\textsubscript{4} emission values recovered some hours after DA (dark–anoxic) treatment.

The proportion of CH\textsubscript{4} (27–52\%) that was oxidized in the mesocosms was within the same range as in several other studies on aquatic macrophytes (King 1996, Lombardi \textit{et al.} 1997, van der Nat and Middelburg 1998b). Ström \textit{et al.} (2005) also found the same proportion (20–40\%) in a \textit{Carex rostrata} stand in peat-forming wetland in southern Sweden, but in two other vascular plants, \textit{Eriophorum vaginatum} and \textit{Juncus effusus}, the oxidized proportion was > 90\%. In many studies a distinct seasonal variation in the proportion of CH\textsubscript{4} oxidized has been observed (Lombardi \textit{et al.} 1997, van der Nat and Middelburg 1998b, Popp \textit{et al.} 2000), but no clear differences in the oxidation percentage in organic sediment between May and September were observed in this work. In sand mesocosms there was no oxidation in September, but at other times the percentage was approximately the same as in organic sediment. This is in accordance with the observation that CH\textsubscript{4} oxidation rate appears to be independent of temperature and is controlled more by CH\textsubscript{4} formation (e.g. Duc \textit{et al.} 2010). According to van der Nat and Middelburg (1998a), variation in CH\textsubscript{4} production rather than variation in CH\textsubscript{4} storage and oxidation determine CH\textsubscript{4} emissions in wetlands dominated by \textit{P. australis} and \textit{Scirpus lacustris}, in accordance with the results in \textit{E. fluviatile} stands are obtained in this study.

Temperature affected the net and potential CH\textsubscript{4} emissions in both bottom types in the mesocosm study (Fig. 3c; \textit{paper III}). Net emission was significantly related to sediment temperature both in the organic and in the sandy bottom. If daily mean air temperature was compared with net CH\textsubscript{4} emission in the organic mesocosm and with the field data from \textit{E. fluviatile} littoral of Lake Pääjärvi (data collected in 1994 and 1995 by Hyvönen \textit{et al.} 1998, see \textit{paper III}), the two model equations obtained were statistically identical (Fig. 3c; \textit{paper III}: fig. 3). This indicates that the temperature response of the littoral CH\textsubscript{4} emission is possibly a permanent feature in the ecosystem. In the sandy bottom, the shoot biomass explained even more of the variation in net CH\textsubscript{4} emission than sediment temperature, indicating that methanogens were limited by substrate availability and were dependent on substrates produced by \textit{E. fluviatile}.

Potential emissions were also dependent on temperature in both organic and sand bottoms, and their temperature response (the slope of the regression model equation) was statistically the same in both bottom types. However, the levels of emission (intercepts of the equations) differed, suggesting again that the methanogens in sand bottoms were more limited by substrate availability. The variation of the shoot biomass of \textit{E. fluviatile} and temperature were intercorrelated, and both factors together influenced the methanogenesis and the CH\textsubscript{4} ventilation through plants into the atmosphere.

The models used to describe the relationship between temperature and potential CH\textsubscript{4} emission (Fig. 3c, eqns 1 and 5) indicate a temperature sensitivity (Q\textsubscript{10}) of 5.6 for organic and 4.4 for sandy bottom, the difference being not statistically significant. The temperature–net emission relationship gave a Q\textsubscript{10} of 4.9 for organic sediment and 1.5 for sand (Fig 3c; linear equation (eqn 6), temperature range 10–20 °C). In the laboratory, methanogens have shown a decreased temperature dependence with decreasing substrate concentration (Westermann \textit{et al.} 1989), and in this study the lower organic matter content and smaller plant biomass in sand mesocosm may also indicate the smaller amount of substrates available for methanogens.

In littoral areas, vegetation has a striking effect on the amount of CH\textsubscript{4} emissions to the air, as can be seen in Lake Ekojärvi (\textit{paper IV}). The plant species, species coverage, biomass and rhizosphere all have a role in mediating the gas into the atmosphere and providing the substrate for methanogens and oxygen for methanotrophs. Therefore, the spatial variation of CH\textsubscript{4} emission in vegetated littorals must be taken into account when estimating the whole-lake and regional CH\textsubscript{4} emissions. The highest CH\textsubscript{4} emissions in Lake Ekojärvi were measured in
P. australis stands, where the daytime CH₄ emission was 1–2 orders of magnitude higher than in the stands of other species (paper IV). P. australis is known to have a pressurized convective flow mechanism that effectively transports oxygen to roots and rhizomes in anoxic sediments and ventilates CH₄ out from the rhizosphere into the air through older or damaged leaves and shoots (Dacey 1981, Armstrong and Armstrong 1991, Brix et al. 1992, 2001, Strand 2002). The pressurization is also affected by solar radiation, temperature and relative humidity. CH₄ emissions in actively growing plants are in daytime usually 2–4 times higher than at night, when CH₄ is passed only by diffusion (Kim et al. 1998, van der Nat and Middelburg 1998a, Brix et al. 2001, Käki et al. 2001).

The CH₄ emission of S. lacustris and E. fluviatile was only 3–12% of the daytime emission of P. australis, which suggests that these species do not have a pressurized convective flow mechanism. This conclusion is also supported by observations by Hyvönen et al. (1998) and van der Nat and Middelburg (1998a) that these species do not have diel variation of CH₄ emission, and by the fact that no correlation between CH₄ emissions and solar radiation was observed. The large difference in proportions (%) of released CH₄ to NPP between P. australis stands and S. lacustris and E. fluviatile stands, which was observed in this study (paper IV), may have been smaller if the CH₄ flux had been estimated on a daily basis, when lower night-time emissions of P. australis and the lack of NPP during the night would have been taken into consideration.

In the compiled CH₄ flux data of all emergent vegetation stands of Lake Ekojärvi, mean shoot weight and mean fetch (MF) explained 90% and mean shoot weight alone 60% of spatial variation. P. australis, that produced most of the CH₄, grew in more sheltered and anoxic sediments than other species, and transferred CH₄ effectively into the air through its pressurized ventilation mechanism. The highest emissions from N. lutea stands were also observed in the most sheltered sites with low MF and the highest cover of leaves per water surface (paper IV). In the stands of S. gramineum and P. nascent the CH₄ emission could not be related to any of the measured variables, which might be linked to the sporadic ebullition from sediments and submerged shoots of vegetation.

Spatial variation of CH₄ emissions in the vegetated littoral of Lake Ekojärvi was influenced by species composition, by the mode of rhizome ventilation in emergent and floating-leaved vegetation, fetch and shoot biomass, indicating the important role of plants as gas conduits from sediment to atmosphere, and as substrate producers for methanogens in sediment. The results for CH₄ variation between different vegetation stands agree with those of Juutinen et al. (2001), who found that CH₄ emissions were highest from permanently flooded Phragmites and Carex marshes in littoral zones of a mesotrophic boreal lake. The results also agree with those of Käki et al. (2001), who measured emissions in the dense P. australis stand of the meso-eutrophic boreal lake Vesijärvi which were within the same range as in this study (midday values 4.8–43.2 mg C m⁻² h⁻¹). Despite the dominating effect of plants, physical factors such as fetch also affect the CH₄ emissions by e.g. wave exposure or sediment resuspension. The mechanisms of these factors were not studied here, but they may have a large influence on e.g. spatial distribution of CH₄ in the water column (Murase et al. 2005, Hofmann et al. 2010).

4.1.3 CH₄ flux — a regional estimate

The regional role of a macrophyte species as a conduit of CH₄ from sediment to atmosphere can be determined by measuring both its specific emission rate and areal coverage (e.g. van der Nat and Middelburg 2000, Ding et al. 2005). The areal coverage of littoral plant species varies considerably with lake size as could be seen in this study (Fig. 4; paper V), and estimating the regional littoral emissions based on only some lake size classes may lead to incorrect results. In the Regional study area of this study (Fig. 1), both the total macrophyte coverage and the area-based net emission rates estimated for P. australis and E. fluviatile stands were so dominant compared to all other species studied...
that they alone emitted 98% of all CH$_4$ during the growing season of 2001 (paper V). Thus the estimation of the regional coverage and CH$_4$ emissions of these two species would have been sufficient to characterize the CH$_4$ emissions from vegetated littorals in the whole region. 

The quite simple models used in the regional study on CH$_4$ emissions (paper V) did not take into account the daytime pressurized convective flow mechanism of *P. australis*, which makes the daytime CH$_4$ emissions higher than night-time. It has been estimated that daytime fluxes may be 2–4, even 10 times higher than those at night when gas flows out only by diffusion and temperatures are lower (Kim *et al.* 1998, van der Nat and Middelburg 1998a, Brix *et al.* 2001, Käki *et al.* 2001, Juutinen *et al.* 2004). Juutinen *et al.* (2004) recommended that daytime measurements should be corrected by a factor of 0.68 to obtain a more reliable estimate of daily CH$_4$ release. Käki *et al.* 2001 also found clear diel variation of emissions in the dense *P. australis* stand in Lake Vesijärvi, although only in August in very shallow littorals (water depth ~ 2 cm), but not in sparser stands growing deeper (> 10 cm water depth) or in the earlier growth stages. Thus variation in the bottom type and in shoot biomass may affect the emissions but they could not be included in the models used in this study. Here, it is assumed that the species-specific emission is solely dependent on temperature. The temperature–CH$_4$ emission models used here are parameterized for the rather dense vegetation stands growing on the organic bottoms (Hyvönen *et al.* 1998, Kankaala *et al.* 2004, paper III), and thus the basic level (intercept) of the model equation is high. Moreover, the areal coverage estimate includes only zone-forming, monospecific plant populations and it is realistic to suppose that their emissions really are within the same range as in the data used when constructing the model (paper V). The use of daily mean temperatures for the total emission estimate may also give more accurate results than the use of mean temperatures of longer time periods.

Northern peatlands with high water table are considered to be significant sources of CH$_4$ in the boreal regions (e.g. Crill *et al.* 1992, Hutunen *et al.* 2003, Bubier *et al.* 2005). CH$_4$ emissions of *P. australis* and *E. fluviatile* stands in vegetated lake littorals were compared with those in natural open peatland areas within the same region and it was found that the total CH$_4$ emissions of the *P. australis* and *E. fluviatile* littorals were 1.3 times higher than those of the open peatlands during the growing season (paper V). This indicates that on a regional level the boreal lake littorals may be even more significant sources of CH$_4$ than peatlands. In their two-year, year-round eddy correlation study of CH$_4$ emissions from subarctic mire with a nearby shallow (maximum depth 1.3 m) lake in Sweden, Jackowicz-Korczyński *et al.* (2010) also found that mid-summer emission rates from the lake were twofold compared to the emission rates from the mire. Area-based annual emissions from the sector influenced by the lake were about 40% higher than from the mire (tall graminoid) sector.

The boreal vegetated lake littorals are diverse, seasonally varying ecosystems with respect to e.g. plant species composition, density, biomass and spatial coverage as well as to the properties of bottom type on which the plants are growing (Fig. 5; e.g. Rørslett 1991, Juutinen *et al.* 2003, Mäkelä *et al.* 2004). Together with highly varying temperature in shallow lake areas, this results in large spatial and temporal variability of benthic CH$_4$ emissions. Thus the total areal coverage of the macrophyte vegetation cannot alone predict the amount of CH$_4$ that vegetated lake littorals emit into the atmosphere. Moreover, because the proportion of species coverage varies greatly between different lake size classes, and hence also the CH$_4$ emissions per unit area vary with the species, the lake size distribution should also be taken into account when making regional estimates.

Scaling the carbon gas flux from the top down or the bottom up between site and regional or global levels contains many sources of error that tend to ignore or underestimate the role of lakes and estuaries as carbon gas sources. Battin *et al.* (2010) concluded that many state-of-the-art inverse models have a coarse spatial resolution and CO$_2$ outgassing from aquatic sources is hence assigned to terrestrial respiration. Juu-
tinen et al. (2009) estimated that in boreal region small lakes have higher CH$_4$ fluxes per unit area than larger lakes. However, small inland lakes and ponds are not usually considered in regional estimates when scaling up from the bottom up approach. This results in underestimation of the role of aquatic environments as a source and sink of the carbon.

4.2 Carbon gas flux in vegetated littorals and climate warming

Temperature has a major effect on CH$_4$ emissions. Especially in lake littorals, where part of the CH$_4$ produced in sediment avoids oxidation by being transported from sediment to atmosphere via plant stems, the effect of increased temperatures on atmospheric emissions can be remarkable. Some emergent macrophytes common in boreal lake littorals, such as P. australis and E. fluviatile, emit large amounts of CH$_4$ during the growing season (papers III, IV). When growing on the organic bottoms, the CH$_4$ emission rate of their stands often has a rather high basic level (intercept of the temperature–emission model equation). Moreover, the temperature sensitivity (Q$_{10}$) of the CH$_4$ emission is rather high in the stands of both species. Hence a relatively small increase in temperature might lead to a high increase in emissions.

Both CO$_2$ and CH$_4$ easily escape from vegetated lake littoral sediments into the atmosphere because of low water depth and macrophyte vegetation. The naturally occurring carbon fluxes in vegetated littorals ranged here between 0 and 14.3 mg C m$^{-2}$ h$^{-1}$ (Table 3; papers I, III, IV). Both CO$_2$ production and CH$_4$ emission were within this range. The amount of gas produced/emitted depended mainly on temperature, although e.g. plant species, shoot biomass and bottom type also had effects of varying strength. When elevated temperatures were used in laboratory incubations (CO$_2$), or when potential gas production was measured (CH$_4$), much higher flux rates up to 79 and 24 mg C m$^{-2}$ h$^{-1}$ were obtained, respectively (Table 3). This indicates that in the warming climate the carbon gas emissions from lake littorals will presumably increase unless other unknown factors contribute to the opposite direction. Using the emission scenarios and temperature–carbon flux models, a 27–29% increase in summer littoral CO$_2$ production and a 60–65% increase in CH$_4$ emission of E. fluviatile stands were predicted for a time interval of 110 years (from 1961–1990 to 2071–2100) (this study, paper I). These estimates agree with literature values. Most recently, Gudasz et al. (2010) estimated that depending on the climate warming scenario used, organic carbon burial into the lake sediment overlaid by mixed water will decrease by 6–15% or 4–27% due to the temperature-driven increase of the carbon mineralisation rate, resulting in increasing emissions. This is quite in line with the estimate for the increase of CO$_2$ production in this study. Bloom et al. (2010) estimated in their large-scale study that due to the temperature increase, CH$_4$ emissions in mid-latitude and Arctic wetland regions have already increased by 7% during the period 2003–2007.

Not only the absolute amounts of carbon gases from lakes are predicted to increase with warming climate. The relative amounts of CO$_2$ and CH$_4$ may also change when temperature increases. According to the temperature–carbon flux models of this study and papers I and III, CH$_4$ production increased with temperature more than CO$_2$ production. Yvon-Durocher et al. (2011) estimated that warming of 4°C would increase the fraction of gross primary production effluxing as CH$_4$ by 20% and the fraction of ecosystem respiration as CH$_4$ by 9%. This suggests that freshwater ecosystems will be in future an even larger source of atmospheric CH$_4$ than earlier expected. Recently, photosynthesis and respiration have also been found to have different temperature dependences at the ecosystem level, respiration increasing more rapidly with temperature than photosynthesis. This reduces the ability of warmed systems to sequester CO$_2$, because more carbon is respired than fixed (Yvon-Durocher et al. 2010). The same conclusion was reached in a study on organic carbon burial by Gudasz (2010).

Although temperature is considered to be a major factor directly affecting the carbon gas fluxes in water-logged wetlands and lake littorals, there are also several other players influ-
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Tranvik et al. (2009) listed nine processes controlling carbon cycling in lakes, and analysed how they will change with changing climate and what will be the effect on greenhouse gas emissions. Most of them, such as watershed hydrology, CO₂ and temperature effects on vegetation, changing seasonality of lake condition (ice cover, stratification etc.), autochthonous production due to littoral vegetation, microbial degradation of organic matter, photodecay and sedimentation, will boost the CO₂ and CH₄ emissions from littoral sediments, with the exception of expected increase in autochthonous production that could decrease the CO₂ flux to the atmosphere (but see above the results of Gudaz et al. (2010) and Yvon-Durocher et al. (2010) indicating increase of carbon flux to the atmosphere despite increasing photosynthetic capacity). Detailed investigation of these processes is urgently needed in order to predict the role of aquatic sediments in carbon gas fluxes in warming climate.

Yhteenenveto

Järven ja merien pohja-alueiden luonnollisesti tuottamat hiilikaasut, hiilidioksidi (CO₂) ja metaaani (CH₄), ovat viime aikoina olleet tutkimuksen kohteina, koska niillä voi olla huomattava osuus ilmaston lämpenemisessä. Hiilidioksidi on happea vaativan hengityksen lopputuote ja metaania tuotetaan suuria määriä hapettomissa olosuhteissa. Erityisesti matalat, kasvillisuuden peittämät ranta-alueet ovat pinta-alaansa nähden näiden kaasujen merkittäviä lähteitä. Metaani, joka on voimakas kasvihuonekaasu, voi kasvillisuuspohjilla siirtää pohjasedimentistä suoraan ilmakehään kasvien varsisolukojen kautta, ja näin välttää hapettumasta hiilidioksidiksi pohjasedimentin pinnassa tai vedessä. Tiedetään, että ympäristön lämpötilan nousu vaikuttaa voimistavasti vesien pohja-alueiden hiilidioksidin ja metaaanin tuottoon, mutta monet muutkin, huomommien tunnetut tekijät säätelevät kuinka paljon kaasuja lopulta kulkeutuu ilmakehään. Tässä yössä on tutkittu boreaalisen alueen järven, erityisesti vesikasvillisuuden peittämiin ranta-alueiden, ja muttovesipohjan tuottamien hiilikaasujen määrää, ajallista ja paikallista vaihtelua sekä vaihtelun vuokattavia tekijöitä. Säätelevistä tekijöistä tutkittiin erityisesti lämpötilan, mutta myös vuodenajajan, pohjan laadun, kasvilajien ym. muuttujien vaikutusta. Pohjan hiilidioksidin tuottonopeudet vaihtelivat kenttäkokeissa välillä 0.1–12.0 mg C m⁻² h⁻¹ ja metaaniemissio malliekoosysteemi- l. mesokosmoskokeessa väliillä 0–14.3 mg C m⁻² h⁻¹. Laboratoriokokeissa hiilidioksidintuotto nousi ainakin 79 mg C m⁻² h⁻¹, kun lämpötilaa nostettiin yli luonnossa esiintyvien vaihtelurajojen. Lämpötila oli hiilikasuvirtoihin eniten vaikuttava tekijä ja se selitti 70–94% kasasuntuoton vaihtelusta järvi-pohjilla ja 51% vaihtelusta muttovesipohjalla. Lämpötila selitti myös 50–90% metaaniemistoon vaihtelusta malliekoosysteemissä. Sen sijaan lämpötila ei vaikuttanut metaaanin hapettumiseen. Kokeissa tutkittiin myös kuuden ilmaversoisen ja kelluslehtisen vesikasvilajien metaaniemissiota tasaisessa lämpötilassa. Ilmaversoisen järvinvirto’on (Phragmites australis) emisiot olivat korkeimmat (k.a. 13.9 ± 4.0 (SD) mg C m⁻² h⁻¹) ja ne korreloivat nettoproduksioon tai ilmankasteen seuraamisessa. Alueellisesti tarkasteltuna ilmaverstoisten ja kelluslehtisten kasvustoissa keskimääräinen metaaniemissio (k.a. 0.5 ± 0.1 (SD) mg C m⁻² h⁻¹) on lähinnä kyseessä yleistä luonnontilanteista, vaikka niitä on olemassa. Kesämääräisissä kasvustoissa on enemmän chemikalia ilmavoimassa ja kasvustoissa on myös kasviensa kasvu. Tämän muuttaessa voimakkaasti kasvikaasujen emissiot kasvavat. Ilmakoosysteemin ja sen karkean työntymisen, jossa kasvu ja hengitys tapahtuvat yhteen, vahvistaa myös ilmastonykyisen kasvillisuuden kasvun kasvu. Keskisammalla kasvillisuus on enemmän kasvillisuusairoja, mutta myös muut kasvumäärät ovat suuremmat. Kokeissa on myös havaittu ilmakoosysteemin ja sen kasvillisuuden vaikutusta kasvillisuusaineiden kasvun kasvuun. Kokeissa on havaittu myös ilmakoosysteemin ja sen kasvillisuuden vaikutusta kasvillisuusaineiden kasvun kasvuun. Kokeissa on havaittu myös ilmakoosysteemin ja sen kasvillisuuden vaikutusta kasvillisuusaineiden kasvun kasvuun.
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References


