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Greenhouse Gas Dynamics in Ice-covered Lakes Across Spatial and Temporal Scales

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Abstract
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Lakes play a major role in the global carbon (C) cycle, despite making up a small area of earth's surface. Lakes receive, transport and process sizable amounts of C, emitting a substantial amount of the greenhouse gases, carbon dioxide (CO_2) and methane (CH_4), into the atmosphere. Ice-covered lakes are particularly sensitive to climate change, as future reductions to the duration of lake ice cover will have profound effects on the biogeochemical cycling of C in lakes. It is still largely unknown how reduced ice cover duration will affect CO_2 and CH_4 emissions from ice-covered lakes. Thus, the primary aim of this thesis was to fill this knowledge gap by monitoring the spatial and temporal dynamics of CO_2 and CH_4 in ice-covered lakes. The results of this thesis demonstrate that below ice CO_2 and CH_4 were spatially and temporally variable. Nutrients were strongly linked to below ice CO_2 and CH_4 oxidation variations across lakes. In addition, below ice CO_2 was generally highest in small shallow lakes, and in bottom waters. Whilst below ice CH_4 was elevated in surface waters near where bubbles from anoxic lake sediment were trapped. During the ice-cover period, CO_2 accumulation below ice was not linear, and at ice-melt incomplete mixing of lake waters resulted in a continued CO_2 storage in bottom waters. Further, CO_2 transported from the catchment and bottom waters contributed to high CO_2 emissions. The collective findings of this thesis indicate that CO_2 and CH_4 emissions from ice-covered lakes will likely increase in the future. The strong relationship between nutrients and C processes below ice, imply that future changes to nutrient fluxes within lakes will influence the biogeochemical cycling of C in lakes. Since catchment and lake sediment C fluxes play a considerable role in below ice CO_2 and CH_4 dynamics, changes to hydrology and thermal stability of lakes will undoubtedly alter CO_2 and CH_4 emissions. Nevertheless, ice-covered lakes constitute a significant component of the global C cycle, and as such, should be carefully monitored and accounted for when addressing the impacts of global climate change.

Keywords: carbon cycle, climate change, cryosphere, carbon dioxide, methane, lakes, winter limnology, methane oxidation, nutrients, catchment

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“Those who contemplate the beauty of the earth find reserves of strength that will endure as long as life lasts. There is something infinitely healing in the repeated refrains of nature -- the assurance that dawn comes after night, and spring after winter.”
― Rachel Carson, Silent Spring

In loving memory of Derek Denfeld
and Peg Spath

List of Papers

This thesis is based on the following papers, which are referred to in the text by their Roman numerals.

I Denfeld B. A., Kortelainen P., Rantakari M., Sobek S., and Weyhenmeyer G. A. (2015) Regional variability and drivers of below ice CO_2 in boreal and subarctic lakes. *Ecosystems,* published online, doi: 10.1007/s10021-015-9944-z.

II Denfeld B. A., Wallin M.B., Sahlée E., Sobek S., Kokic J., Chmiel H.E., and Weyhenmeyer G. A. (2015) Temporal and spatial carbon dioxide concentration patterns in a small boreal lake in relation to ice cover dynamics. *Boreal Environ. Res.,* 20: 679-692.

III Canelhas M. R., Denfeld B. A., Weyhenmeyer G. A., Bastviken, D., and Bertilsson S. (2015) Methane oxidation at the water-ice interface of an ice-covered lake, Submitted.

IV Denfeld B. A., Canelhas M. R., Weyhenmeyer G. A., Bertilsson S., Eiler A., and Bastviken, D. (2016) Constraints on methane oxidation in ice-covered boreal lakes. Submitted.

Additional Papers

In addition to the papers included in this thesis I have also contributed the following papers:

- Kokic J., Wallin M.B., Chmiel H.E, Denfeld B. A., and Sobek S. (2015) Carbon dioxide evasion from headwater systems strongly contributes to the total export of carbon from a small boreal lake catchment. *J. of Geophys. Res. Biogeosciences.,* 120: 13-28.

- Chmiel H.E., Kokic J., Denfeld B. A., Einarsdóttir K., Wallin M.B., Isidorova A., Koehler B., Bastviken D., Ferland M.-E., and Sobek S. (2015) The role of lake sediments in the carbon budget of a small boreal lake. Submitted.

Contents

Abbreviations

C	carbon
CH_4	methane
CO_2	carbon dioxide
DIC	dissolved inorganic carbon
DOC	dissolved organic carbon
GHG	greenhouse gas
MOB	methane-oxidizing bacteria
O_2	oxygen
OM	organic matter
pCO_2	partial pressure of carbon dioxide
TOC	total organic carbon

Introduction

Carbon cycle

Carbon (C) is an abundant element on planet earth and combined with other elements, form the basic building blocks of life. C is naturally cycled between the land and the atmosphere. In the atmosphere C can be found in the gaseous form as carbon dioxide (CO_2) and methane (CH_4). Both CO_2 and CH_4 are greenhouse gases (GHG) that keep heat from escaping earth's atmosphere. Although the concentration of CH_4 in the atmosphere is one hundredfold less than CO_2, CH_4 is 28 times more efficient in trapping heat than CO_2 (IPCC 2013). Since the beginning of the industrial era, human activities have increased the amount of GHG emitted into the atmosphere at a rate above that of the natural earth cycle. Fossil fuel burning, land use change and agricultural practices are the main perpetrators of this increase and the recent notable climate changes (IPCC 2013). In response to increased GHG in the atmosphere, earth is experiencing rising average temperatures, shifts in snow and rain patterns and more extreme climate events, such as floods, droughts and wildfires (IPCC 2013).

Natural ecosystems also cycle C and emit CO_2 and CH_4 into the atmosphere. The natural ecosystem of lakes offer an example, as they receive, transport and process C, emitting a substantial amount of CO_2 and CH_4 into the atmosphere (Cole et al. 2007; Tranvik et al. 2009). At the same time as being a source of C to the atmosphere, organic carbon that sinks to the bottom of the lake can be stored in lake sediments over geological time scales (Kortelainen et al. 2004). Although lakes only make up a small area of earth's surface, they play a major role in the global C cycle (Battin et al. 2009). Lakes have been termed as sentinels, integrators and regulators of climate change, further emphasizing the role they play in global biogeochemical cycles (Williamson et al. 2008). Recent climate change due to human activities has altered the hydrological, biogeochemical and ecological processes that affect rates of C processing in lakes (Benoy et al. 2007). Yet, how these changes will alter the amount of CO_2 and CH_4 emitted from lakes into the atmosphere remains largely unknown. Thus, assessing the impact of climate change on C processing and associated GHG emissions from lakes is an important undertaking.

CO_2 concentrations in lakes

The CO_2 concentrations in lakes reflect the balance between external and internal fluxes (**Figure 1a**). Primary production and decomposition of organic matter (OM) are two processes that make up a large part of the internal CO_2 flux. The main primary producers are photosynthetic organisms (phytoplankton, macrophytes and benthic algae) that undergo a chemical process which converts CO_2 into new OM, using nutrients and light as energy. The reverse process is decomposition, where OM is recycled back into inorganic compounds such as CO_2. In lakes decomposition of OM into CO_2 can occur via respiration, photochemical mineralization and CH_4 oxidation (described below). Respiration is a process by which heterotrophic organisms (bacteria, zooplankton and benthic invertebrates) in aquatic systems cannot fix C and therefore consume C for growth, releasing water and CO_2 as byproducts. Although proportionally less so, photosynthetic organisms respire CO_2 as well. In photochemical mineralization dissolved organic carbon (DOC) is reduced by solar ultraviolet radiation, forming a range of photoproducts. Photoproducts can be inorganic compounds (e.g., CO_2) from direct photochemical mineralization of C (Granéli et al. 1996) or can remain as organic molecules that are susceptible to further biological decomposition (Bertilsson and Tranvik 1998).

Many lakes are classified as net heterotrophic, where respiration exceeds primary production, and therefore these systems produce more CO_2 than is consumed (Cole et al. 1994; del Giorgio and Peters 1994). In the case of net heterotrophy, the partial pressure of CO_2 (pCO_2) in the lake is greater than that in the atmosphere, thus, CO_2 is emitted into the atmosphere. To achieve net heterotrophy, in addition to autochthonous DOC (i.e. derived in the lake), lakes are subsidized by an input of allochthonous DOC (i.e. derived from the catchment) (Lennon 2004). Lakes can further be sourced with CO_2 directly via stream and groundwater inputs (Striegl and Michmerhuizen 1998; Stets et al. 2009; Weyhenmeyer et al. 2015).

CH_4 concentrations in lakes

As was the case for CO_2, CH_4 concentrations in lakes also reflect the balance between external and internal fluxes (**Figure 1a**). The net balance of CH_4 is determined by the interplay between methanogenesis, the production of CH_4, and CH_4 oxidation, the breakdown of CH_4. Methanogenesis is exclusively carried out by archaea (single-celled microorganisms) under anaerobic conditions (i.e. without oxygen (O_2)). CO_2 and other single C compounds, in addition to acetate, are used by methanogens, microorganisms that produce CH_4 (Kirchman 2011). On the other hand, CH_4 oxidation has been found to

occur in both aerobic (i.e. with O_2) and anaerobic environments (Bastviken, 2009, referenced within). During aerobic CH_4 oxidation, methane-oxidizing bacteria (MOB) use CH_4 as a C and energy source and O_2 as an electron acceptor, with CO_2 as the typical end product. In lakes, sediments are the main site of CH_4 production. Since CH_4 production is the terminal redox reaction in the decomposition of OM, processes using alternative electron acceptors (e.g. NO_3-, Mn^{4+}, Fe^{3+}, SO_4^{2-}) are energetically more favorable. Therefore, CH_4 production is restricted to environments with low concentrations of alternative electron acceptors yet sufficient substrate supply; such is the case in lake sediments. Although aerobic CH_4 oxidation has been found to occur throughout the lake, it is most extensive at the aerobic-anaerobic interface (Bastviken et al. 2002; Kankaala et al. 2006).

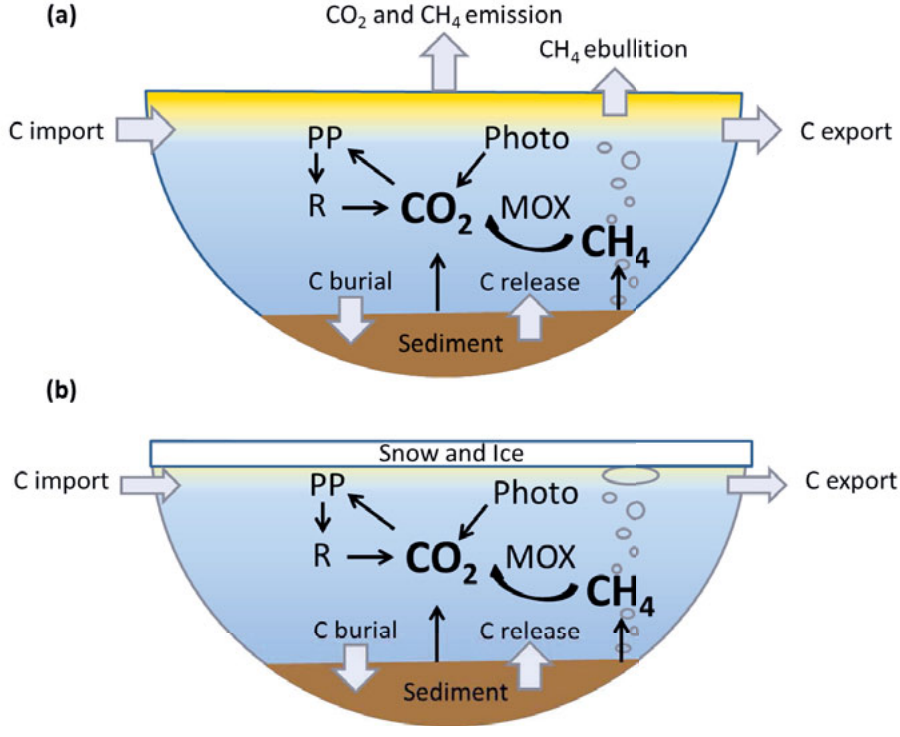

Figure 1 External and internal carbon (C) fluxes (grey arrows) and internal fluxes of carbon dioxide (CO_2) and methane (CH_4) consumption and production (black arrows) in a lake (a) during the open water period and (b) during the ice cover period. Abbreviations are as follows: primary production (PP), respiration (R), methane oxidation (MOX) and photochemical mineralization (Photo).

CO_2 and CH_4 emission pathways

The amount of CO_2 and CH_4 emitted from the lake into the atmosphere depends on the gas concentration in the water column and the gas transfer velocity at the water-atmosphere interface. The gas transfer velocity is determined by turbulent energy mixing between the surface water and atmosphere (Zappa et al. 2007; Vachon et al. 2010) and has been found to differ for CO_2 and CH_4 (Prairie and del Giorgio 2013; Rantakari et al. 2015). In stratified lakes, i.e., where surface and bottom waters become disconnected with warmer waters found in the surface of the lake, CO_2 and CH_4 in surface waters are emitted into the atmosphere via diffusion (Boehrer and Schultze 2008). During the seasonal spring and autumn lake water mixing periods, gases accumulated in bottom waters during stratification are mixed up to the surface waters and subsequently emitted into the atmosphere (López Bellido et al. 2009). In addition to diffusion and water mixing, CH_4 has two further emission pathways; ebullition and plant mediation. In ebullition CH_4 produced in sediments is quickly bubbled through the water column and successively emitted into the atmosphere. In plant mediation CH_4 is emitted from lake sediments into the atmosphere through rooted emergent plants. In both pathways, ebullition and plant mediation, zones of potential CH_4 oxidation are bypassed.

CO_2 and CH_4 dynamics in ice-covered lakes

Many lakes in the northern hemisphere are ice covered for a large portion of the year (Prowse et al. 2012). Ice and snow on lakes act as a barrier to drivers of physical and biological processes such as atmospheric exchange, water column mixing and light penetration (Prowse et al. 2012). The ice-cover duration shapes the physical structure of the water column (as disscused in Bertilsson et al. 2013) and in turn influences biological CO_2 and CH_4 accumulation below ice (**Figure 1b**). Since water is most dense at around 4˚C, inverse stratification, i.e., where surface and bottom waters become disconnected with cooler surface waters, can establish below ice (Boehrer and Schultze 2008). In bottom waters, lake sediments drive circulation and heat flux, while in surface waters penetration of light is the main driver (Bengtsson 1996; Kirillin et al. 2012). OM degradation (i.e. CO_2 and CH_4 production) at the sediment-water interface leads to a build-up of CO_2 and CH_4 in bottom waters (Striegl and Michmerhuizen 1998; Kortelainen et al. 2006; Ducharme-Riel et al. 2015). In surface waters light availability below ice determines the balance between respiration and primary production, and thus CO_2. In the late winter period, primary production (i.e. CO_2 consumption) immediately below ice may be more favorable, as increase in solar radiation and snow melt allow light to penetrate surface waters (Belzile et al.

2002; Baehr and DeGrandpre 2004; Huotari et al. 2009). Further, CH_4 concentrations in surface waters may be elevated as CH_4 released from lake sediments, via ebullition gets trapped at the water-ice interface (Walter et al. 2006). However, if this CH_4 is subject to CH_4 oxidation prior to ice-melt, surface water CH_4 concentrations may be reduced (Greene et al. 2014) and in turn surface water CO_2 concentrations increased. Apart from internal processes, surface and subsurface inflows of OM, CO_2 and CH_4 have been found to be important to below ice CO_2 and CH_4 dynamics during early and late winter (Karlsson et al. 2013; Miettinen et al. 2014).

At ice-melt, CO_2 and CH_4 gas accumulated during winter is emitted into the atmosphere (Striegl et al. 2001; Ducharme-Riel et al. 2015). This emission can be substantial as Karlsson et al. (2013) have recently estimated that in subarctic lakes up to 56 % and 84 % of the total annual CO_2 and CH_4 emission from an individual lake, respectively, can occur at ice-melt. CH_4 and CO_2 emissions during ice-melt have been found to be rapid and dynamic (López Bellido et al. 2009) and in some cases incomplete water column mixing occurs (Huotari et al. 2009). Further, across years, the stability of stratification and the depth of water column mixing at ice-melt, and hence CO_2 and CH_4 emissions, have been found to vary for individual lakes (Huotari et al. 2009).

Impacts of climate change on ice-covered lakes

In many parts of the northern hemisphere temperature and precipitation have increased due to enhanced GHG forcing in the atmosphere (Serreze et al. 2000, references within). In particular, for ice-covered lakes, warming has been accelerated (O'Reilly et al. 2015) leading to an observed decrease in lake ice cover duration (Magnuson et al. 2000). Long-term ice record across the northern hemisphere have indicated that ice thickness, autumn freeze-up, spring break-up and snow conditions are changing (Strum and Liston 2003). These changes are likely to continue into the future having effects on physical and chemical lake conditions (e.g. Weyhenmeyer 2009) and hydrologic connectivity of the surrounding catchment (e.g. Spence et al. 2015). In addition, below ice bacterial communities will have to adapt to the changes in snow and ice conditions, having consequences on below ice biogeochemical processes (Bertilsson et al. 2013). It is still largely unknown how reduced ice cover duration will alter CO_2 and CH_4 emissions from ice-covered lakes.

CO_2 and CH_4 across different scales

In order to understand how reduced ice cover duration will affect GHG emissions from ice-covered lakes requires research that spans across a variety of scales from micro-scale processes (e.g. respiration, primary production) to a regional set of lakes. Processes, such as respiration, have been studied in individual lakes for many decades but temporal and spatial variability of respiration has made global and regional estimates difficult. More recently, advancements in technology such as remote sensing and sensor development have allowed for micro-scale processes to be more accurately scaled-up (Melack et al. 2011; Crawford et al. 2014). Typically broad regional and global scale estimates of lake elements are developed with the use of statistically significant relationships between easily made measurements (e.g. landscape characteristics) and lake-specific concentrations (e.g. CO_2) (e.g. Raymond et al. 2012). Although this approach offers an opportunity to understand complex scientific processes on a broader scale, many assumptions are made and therefore interpretations should be made with caution. Further, as technology and scientific knowledge advances, current global estimates should be revisited and refined to reduce uncertainty and increase accuracy of research findings.

Presently, a few global estimates of inland water CO_2 (Cole et al. 2007; Tranvik et al. 2009; Aufdenkampe et al. 2011; Raymond et al. 2013) and CH_4 emissions (Bastviken et al. 2011; Wik et al. 2016) have been made. These estimates have been fundamental in advancing our understanding of the global C cycle in lakes. However, these estimates have a temporal biased towards the open water season and in some cases neglect the ice-cover period altogether. Thus, in order to improve estimates of CO_2 and CH_4 emissions, research on CO_2 and CH_4 dynamics in lakes from ice-on to ice-off across spatial scales is needed.

Aims of the Thesis

The primary goal of this thesis was to gain insight on the spatial and temporal dynamics of CO_2 and CH_4 in ice-covered lakes. Thereby, a better understanding of how reduced ice cover duration will affect GHG emissions from ice-covered lakes was obtained.

Specific goals were to determine:

- Regional and catchment scale drivers of below ice CO_2 and CH_4 (Papers I & IV) How does below ice CO_2 vary across a diverse set of lakes located in Sweden and Finland? How does below ice CH_4 oxidation vary between lakes characterized by varying water chemistry and lake morphometry?

- Within-lake CO_2 and CH_4 dynamics (Papers I-III) How does below ice CO_2 and CH_4 vary spatially within a lake? Does CH_4 oxidation occur at the water-ice interface near ebullition bubbles trapped below the ice?

- Temporal development of CO_2 from ice-on to ice-off (Paper II) Does CO_2 linearly accumulate in lakes below ice? At ice-melt is the CO_2 accumulated during the ice cover period emitted into the atmosphere?

Methods

Study sites

The study site(s) for each individual paper of this thesis ranged in spatial scale; 506 lakes across Sweden and Finland (Paper I), seven lakes in Uppland county, Sweden (Paper IV), Lake Gäddtjärn (Paper II) and Lake Erken (Paper III) (**Figure 2**).

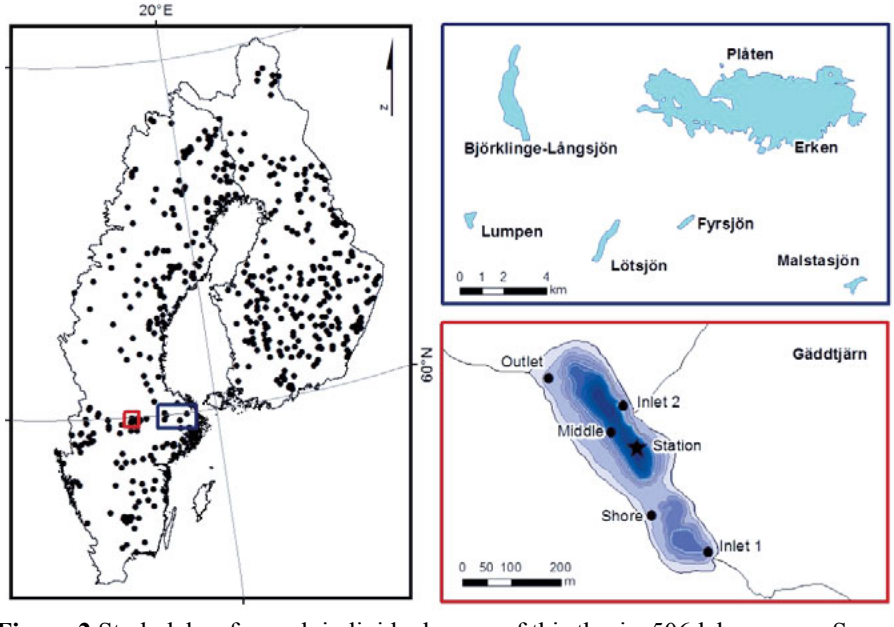

Figure 2 Study lakes for each individual paper of this thesis; 506 lakes across Sweden and Finland (Paper I-black box), Lake Gäddtjärn (Paper II- red box), Lake Erken (Paper III-blue box) and seven lakes in Uppland county, Sweden (Paper IV-blue box. Note distance between lakes is not to scale).

In paper I, the 506 lake database comprised lakes from the Swedish National Lake Inventory Programme (http://www.slu.se/vatten-miljo), and the published studies of Sobek et al. (2003), Rantakari and Kortelainen (2005) and Kortelainen et al. (2006), and spanned gradients in lake size, nutrient concentration and humic matter content. In paper II, Lake Gäddtjärn, a small boreal lake (lake area 0.64 km^2, mean depth 3.8 m) located in central Sweden (59.86 ˚N, 15.18 ˚E) was intensively sampled during the ice cover peri-

od. In paper III, multiple samplings below ice were carried out at Lake Erken (59.85˚ N, 18.58˚ E), a historically monitored, large lake (lake area 24 km^2, mean depth 9 m). In paper IV, seven lakes located in Uppland County, Björklinge-Långsjön, Erken, Fyrsjön, Lumpen Lötsjön, Malstasjön, and Plåten, were sampled once during the ice cover period. A schematic overview of the associated spatial and temporal scale of the four individual papers is given in **Figure 3.**

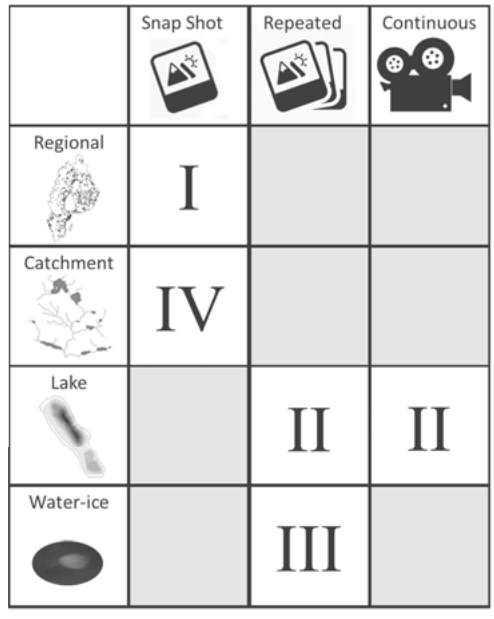

Figure 3 Schematic overview of the spatial (vertical axis) and temporal (horizontal axis) scale from which below ice GHG dynamics were studied in each individual paper of this thesis. One time 'snap shot' sampling on a regional (Paper I) and catchment scale (Paper IV), repeated and continuous sampling in one lake (Paper II) and repeated sampling at the water-ice interface (Paper III).

Lake characteristics

Lake characteristics, including lake morphometry, catchment characteristics, landscape position, and climate variables, were derived in a geographical information system. Lake morphometry (e.g. lake area, volume, average depth) and catchment characteristics (e.g. catchment area and % land cover type in the catchment) were acquired from topographic maps combined with land use data on satellite images using the Arc View georeferencing software. As an indicator of landscape position, lake hydrology was defined using the protocol described in Martin and Soranno (2006) where each lake was assigned a category for the landscape position metric using the Swedish

(VIVAN 2007, 298,215 lakes and 933,675 streams) and Finnish (53,511 lakes and 40,051 streams) network of rivers and lakes for flow-based modeling database. Average annual air temperature for each lake was based on an averaged 1961-90 temperature value (from Swedish meteorological and hydrological institute for Sweden and Finnish meteorological institute for Finland). Ice duration was calculated by using an air temperature function, which was calibrated and validated for Swedish lakes (Weyhenmeyer et al. 2013).

Field sampling

Field sampling was carried out from ice-on to ice-off (Paper II-IV). A hole was drilled in the ice and water was collected at different depths using a Ruttner sampler. To collect water at fine-scale depths (0-60 cm below ice) at the water-ice interface an in-house constructed Below ice LAke MONitoring (BLAMON) sampler was used (Paper III). In addition, depth profiles of dissolved O_2, water temperature and specific conductivity were recorded at 1-meter intervals using an HQ40d Portable Multi-parameter sonde (HACH). For Lake Gäddtjärn, CO_2 concentration, dissolved O_2, pH, water temperature and light intensity were automatically monitored over the ice cover and ice-melt period (Paper II).

Greenhouse gas analyses

All CO_2 and CH_4 measurements collected during the thesis (Paper II-IV) were directly made using the headspace equilibration technique. Briefly, the headspace technique involved filling a polypropylene syringe with bubble free lake water. A headspace of ambient air was then introduced and the syringe was shaken for at least one minute to equilibrate the dissolved gas from the water into the headspace. The resulting headspace was either directly measured (for CO_2) or transferred to a closed serum vial filled with a saturated NaCl solution to preserve the sample until it was analyzed (for CH_4, e.g. Bastviken et al. (2010)). Headspace CO_2 was measured on a portable infrared gas analyzer (EGM-4, PP Systems Inc, U.S) and the corresponding pCO_2 and CO_2 concentration was calculated according to Henry's law presented by Weiss (1974) correcting for temperature and the amount of CO_2 added to the syringe by the ambient air (e.g. Sobek et al. 2003). Headspace CH_4 was measured on a gas chromatograph (Agilent Technologies 7890A GC Systems) equipped with a flame ionization detector. CH_4 concentration was calculated according to Henry's law, correcting for temperature according to Lide and Frederikse (1995) and the amount of CH_4 in ambient air.

Published CO_2 data was also used (Paper I), where CO_2 was based on alkalinity, pH, water temperature and altitude according to Weyhenmeyer et al. (2012) and from total inorganic carbon, pH and water temperature, using Henry's law constants corrected for temperature and atmospheric pressure (Plummer and Busenberg 1982). Further, hourly CO_2 was measured (Paper II) using the submersible autonomous moored instrument for CO_2 (Sunburst Sensors, SAMI2) suspended in the water column at 2 m depth below the ice.

Below ice CO_2 accumulation and emission at ice-melt

Below ice CO_2 accumulation and loss was quantified (Paper II). Whole-lake CO_2 storage (mol CO_2) was calculated as the sum of integrating the measured CO_2 depth profile with the volume of each corresponding depth layer (Michmerhuizen et al. 1996). Whole-lake accumulation and loss of CO_2 (mol CO_2 d^{-1}) was then calculated as the difference in CO_2 storage between sampling occasions divided by the number of days between the sampling. Further, the relative amount of CO_2 accumulated below ice that was released during spring melt (%) was calculated as the ratio of CO_2 storage leaving the lake during ice-melt to CO_2 storage accumulating in the lake during the ice-cover.

CO_2 emission (CO_{2_E}) was calculated utilizing the following equation (Paper I-II):

$$CO_{2_E} = k \, x \, (CO_{2_w} - CO_{2_a}) \qquad (1)$$

where k is the gas transfer velocity and $(CO_{2_w} - CO_{2_a})$ accounts for the difference between CO_2 concentrations in the water and in the air. The gas transfer velocity was estimated from k_{600} normalized to a temperature-dependent Schmidt number for CO_2 (600 at 20˚C) according to (Jähne and Dietrich 1987). k_{600} was derived from three methods; wind speed based on the relationship from Cole and Caraco (1998) , floating chambers measurements from Krenz (2013) and lake area adjusted measurements from Raymond et al. (2013).

CH_4 oxidation

Below ice CH_4 oxidation potential was assessed *in vitro* by incubating CH_4 amended lake water in cold temperatures (~2 ˚C) and in the dark, similar to the conditions found for a snow and ice-covered lake (Paper III & IV). CH_4 oxidation was tracked as the change in CH_4 over time and the corresponding CH_4 oxidation rate was determined from the slope of the linear regression of the natural logarithm of CH_4 against time (following Utsumi et al. 1998).

The potential rate of *in situ* CH_4 oxidation in the lake (mg C m^{-3} d^{-1}) was calculated by multiplying the CH_4 oxidation rate of the incubation by the measured *in situ* CH_4 concentration (Paper III), assuming that CH_4 oxidation is CH_4 substrate dependent.

Chemical analyses

Additional water chemistry analyses, DOC (Paper I-IV), dissolved inorganic carbon (DIC) (I-III), nutrients (Paper I, III & IV) and δ ^{13}C-CH_4 stable isotope (Paper III & IV) were made. Water samples for DOC were filtered through a precombusted 0.7 µm Whatman GF/F glass fiber filter and analyzed on a total organic carbon (TOC) analyzer. In paper I, published TOC data was seen as equivalent to DOC, since boreal lakes usually contains 97 % ± 5 % DOC (von Wachenfeldt and Tranvik 2008). For DIC analysis, 12 mL glass vials were filled with bubble free water and analyzed using a TOC analyzer equipped with a membrane-based conductivity detector. Water for the analyses of inorganic nutrients, nitrate (NO_3-), phosphate (PO_4^{3-}) and sulfate (SO_4^{2-}), was filtered through pre-rinsed 0.2 µm Supor 200 filters (Pall Corporation, Port Washington, NY, USA) and measured by ion exchange chromatography on an ion-chromatograph (883 Basic IC plus, Metrohm). Stable isotope analysis of δ ^{13}C-CH_4 (i.e. $^{13}C/^{12}C$) of the water (Paper III) and the headspace gas (Paper IV) was analyzed at the Stable Isotope Facility at UC Davis following standard procedures using isotope ratio mass spectrometer.

Bacterial analyses

Bacterial analyses were conducted to provide a link between CH_4 oxidation potential and realized function. Bacterial abundance (Paper III & IV) and bacterial community composition (Paper III & IV) were carried out for *in situ* lake water and incubated lake water. Bacterial abundance was measured by volumetric cell counting using flow cytometer, where prior to analysis cells were fixed and stained according to del Giorgio et al. (1996). Cell counts were analyzed using Flowing Software version 2.5 (Perttu Terho, Centre for Biotechnology, Turku Finland). Bacterial communities were analyzed from amplicon sequences of bacterial 16S rRNA genes using next generation Illumina sequencing for the readout. Raw sequence data was analyzed and quality filtered with an in-house pipeline (Sinclair et al. 2015) and then assigned to operational taxonomic units (OTUs) using a 97 % identity clustering. An overview of the sampling methods used in each individual paper is given in **Table 1.**

Table 1 Overview of sampling and analyzing strategies for water chemical and biological data (see text for description) used in each individual paper of this thesis. Abbreviations are as follows: F for field sampling, I for incubation, M for manual sampling, A for automatic sampling, P for published data and nd for not determined.

Greenhouse Gas Analyses				
Paper	CO_2	CH_4	CH_4 oxidation	Gas transfer
I	F-P	nd	nd	F-P
II	F-M&A	nd	nd	F-M
III	F-M	F-M	I-M	nd
VI	I-M	F-M	I-M	nd
Chemical Analyses				
Paper	DOC	DIC	Nutrients	$\delta\ ^{13}C\text{-}CH_4$
I	F-P	F-P	F-P	nd
II	F-M	F-M	nd	nd
III	F&I-M	I-M	F&I-M	I-M
VI	F-M	nd	I-M	I-M
Biological Analyses				
Paper	Abundance	Sequencing		
I	nd	nd		
II	nd	nd		
III	F&I-M	F&I-M		
VI	I-M	I-M		
Lake Conditions				
Paper	O_2	pH	Water temp.	Conductivity
I	nd	F-P	F-P	F-P
II	F-M&A	F-M&A	F-M&A	F-M&A
III	F-M	nd	F-M	nd
VI	F-M	F-M	F-M	F-M

Statistics

Standard statistical test were used to assess the significance of the data (e.g. t-test, ANOVA; Paper I-IV). Normality of the data was tested using Shapiro-Wilk's test ($p < 0.05$ indicating data are non-normally distributed), and in cases where normality was not met, data were transformed or non-parametric test were used (e.g. Wilcoxon test, Spearman's rho).

A spatial analysis of below ice CO_2 across 506 lakes in Sweden and Finland was preformed (Paper I). For determining the relationship between below ice CO_2 (dependent variable) and below ice lake chemistry, lake morphometry and ice cover variables (independent variables), Pearson's correlation coefficients were used, where all the input data were log-transformed due to non-normal distribution. The independent variables were ranked according to their relevance in explaining below ice CO_2 using multivariate partial least square regression (Wold et al. 1993). Below ice CO_2 within-lake spatial variation was also investigated (Paper II). To test if below ice CO_2 was statistically differed between surface and bottom waters manually-measured CO_2 from bottom and surface waters were compared using a matched-pair t-test. To test if horizontal surface water CO_2 was variable over the ice cover period we used a two way ANOVA, where location and time were set as the two independent variables and CO_2 concentration in the surface waters was set as the dependent variable. To identify temporal trends in below ice CO_2 a Mann-Kendall trend test was applied, based on the non-normal distribution of the continuous CO_2 measurements (Paper II). The Mann-Kendall trend test was also used to quantify the rate of change in the below ice CO_2 concentration (in days) by taking the Theil slope.

Results and Discussion

Spatial variability of below ice CO_2 and CH_4 across lakes (Paper I & IV)

On regional scale nutrient concentrations, phosphorus and nitrogen, and lake depth were the most important variables explaining variations in below ice pCO_2 (Paper I). Together water chemistry and lake morphometry explained 53 % of the site-to-site variation in below ice pCO_2. The highest pCO_2 was found in small shallow lakes and deep bottom waters, where highest nutrients were also found. Across boreal lakes in Finland, CH_4 concentrations below ice have similarly been related to lake depth and nutrients, with highest CH_4 concentrations found in surface waters of smaller humic lakes and bottom waters of large humic lakes (Juutinen et al. 2009). High CO_2 and CH_4 in small shallow lakes could reflect that these lakes generally receive more external CO_2, CH_4, and OM compared to large lakes. Further, since small shallow lakes have a larger sediment surface area-to-water volume ratio and a smaller distance between sediments and surface waters, it is possible that benthic derived CO_2 and CH_4 further enhances water column CO_2 and CH_4 concentrations (Ducharme-Riel et al. 2015). While in deep lakes benthic derived CO_2 and CH_4 remains in bottom waters as a thermally stratified water column disconnects bottom waters from surface waters. The positive relationship between water chemistry and pCO_2 could also suggest that the availability and quality of OM below ice promotes degradation and thus CO_2 and CH_4 production.

When comparing CH_4 oxidation potential across lakes an unexpected variability was found. Out of the seven ice-covered lakes studied, three had a potential for CH_4 oxidation while CH_4 oxidation in the other four lakes was not observed (Paper IV). Although MOB were detected in all seven lakes sampled at the start of the incubation, a significant increase in the relative abundance of MOB was only observed in the three lake water incubations where oxidation was observed. Variables shown to limit CH_4 oxidation have been previously reviewed (Hanson and Hanson 1996; Bastviken 2009) and include CH_4 availability, temperature, O_2 availability, pH, salinity, light intensity, zooplankton grazing and nitrogen (NH_4^+ or NO_3-). However a clear relation between any of these variables and CH_4 oxidation was not found in our study, suggesting that CH_4 oxidation was limited by something other

than what has previously been reported. Rather, based on our results, we propose that phosphate and bacterial community interactions, at least partially, limits MOB growth and thus CH_4 oxidation. Since MOB are considered slow growing bacteria with low growth rates (Van Bodegom et al. 2001) they tend to be out-competed for nutrients by faster growing heterotrophic bacteria. Potentially the three lakes where CH_4 oxidation was observed had enough phosphate available to sustain both the fast growing heterotrophs and the slow growing MOB.

Within-lake spatial variability of below ice CO_2, and CH_4 (Paper I-III)

The below ice vertical CO_2 variability (i.e., difference in CO_2 concentrations between surface and bottom waters) was greater than horizontal CO_2 variability (i.e., difference in CO_2 concentrations between spatial surface water sites) (Paper II). Vertical CO_2 variability increased throughout the winter since CO_2 accumulated faster in bottom waters than in surface waters. An important source of CO_2 to bottom waters were the sediments, as indicated by CO_2 increasing with water depth (Paper I-III) and in line with earlier reports of sediment respiration being the main source of CO_2 emission from boreal lakes (Kortelainen et al. 2006). Sediments represent an environment that is highly enriched in both C and nutrients for microbial growth and respiration, leading to substantial CO_2 production (del Giorgio et al. 1999). Over winter a change in redox conditions at the sediment surface can cause additional nutrients and C to be released from the sediments into bottom waters (Mortimer 1941; Gonsior et al. 2013) likely enhancing microbial respiration in bottom waters. On the other hand, surface water CO_2 below ice can be quite dynamic for a number of reasons including internal seiches (Baehr and Degrandpre 2002), venting of gases through ice cracks (Phelps et al. 1998) and solar driven convection (Bertilsson et al. 2013). In addition, CH_4 oxidation (Greene et al. 2014) and primary production (Baehr and Degrandpre 2004) below the ice may influence surface water CO_2 concentration variations.

Similar to the below ice vertical CO_2 gradient, most studies on below ice vertical CH_4 gradient have found higher concentrations in hypoxic bottom waters compared to the surface (Kortelainen et al. 2000; Bastviken et al. 2002; Karlsson et al. 2013). However, for the lake studied in this thesis, Lake Erken, bottom waters had consistently low CH_4 concentrations (Paper III). Since bottom waters were oxygenated throughout the winter in Lake Erken, it is likely reduced CH_4 production and potentially increased aerobic CH_4 oxidation kept CH_4 concentrations low. However, in the same lake at

the water-ice interface CH_4 concentrations were elevated near bubbles trapped below the ice. Bubbles rapidly released from lake sediments via ebullition that become trapped at the water-ice interface can contain high concentrations of CH_4 (Walter et al. 2006). Evidence was found to support the concept that CH_4 dissolves from these bubbles into the surrounding water column. At highly resolved depths (0-60 cm) highest CH_4 was found at 0 cm below the ice and decreased with depth along the upper 20 cm of the water column. The amount of CH_4 dissolved in the water column and subsequently the amount oxidized below ice will determine the fraction of CH_4 that is emitted into the atmosphere at ice-melt.

Despite that fact that CH_4 is available in waters just below ice, previous studies have assumed that CH_4 oxidation at the water-ice interface is negligible due to the slowdown or inactivity of MOB in the cold waters found there (Michmerhuizen et al. 1996; Phelps et al. 1998; Kankaala et al. 2006). However, these studies incubated water for only 24 hours. After several days of *in vitro* incubations of water from Lake Erken, CH_4 oxidation was found to occur at the low temperatures similar to the water-ice interface (Paper III). Therefore, CH_4 oxidation in cold waters may be a slow process but, given enough time, has the potential to reduce CH_4 concentrations in surface waters below the ice (e.g. Greene et al. 2014). Further, the MOB group *Methylococcaceae* increased in abundance throughout the incubation, providing evidence that some strains of MOB are active and adapted to low temperatures.

Temporal development of CO_2 from ice-on to ice-off (Paper II)

Tracking continuous CO_2 concentration and whole-lake CO_2 storage from ice-on to ice-off in Lake Gäddtjärn (Paper II) revealed that CO_2 did not constantly increase throughout the winter period (**Figure 4**). CO_2 concentration and whole-lake CO_2 storage increased mainly in early winter while in late winter the concentrations remained relatively constant after maximum ice thickness had been reached. Further, factors driving the temporal development of CO_2 below ice differ slightly between surface and bottom waters (Paper I & II). In agreement with previous studies (Striegl et al. 2001; Karlsson et al. 2013) catchment CO_2 inputs (surface and subsurface flow) and biological in-lake CO_2 production likely contribute to surface water CO_2 accumulation in early winter. As winter develops, minimized catchment CO_2 inputs combined with reduced bacterial respiration, due to decreased substrate quantity and bioavailability, decreases the rate of surface water CO_2 accumulation. In bottom waters CO_2 continues to accumulate throughout

winter, mainly driven by sediment OM degradation. However, as CO_2 increases in bottom waters overtime, less CO_2 is able to diffuse from the sediments, resulting in reduced CO_2 accumulation rates later in winter.

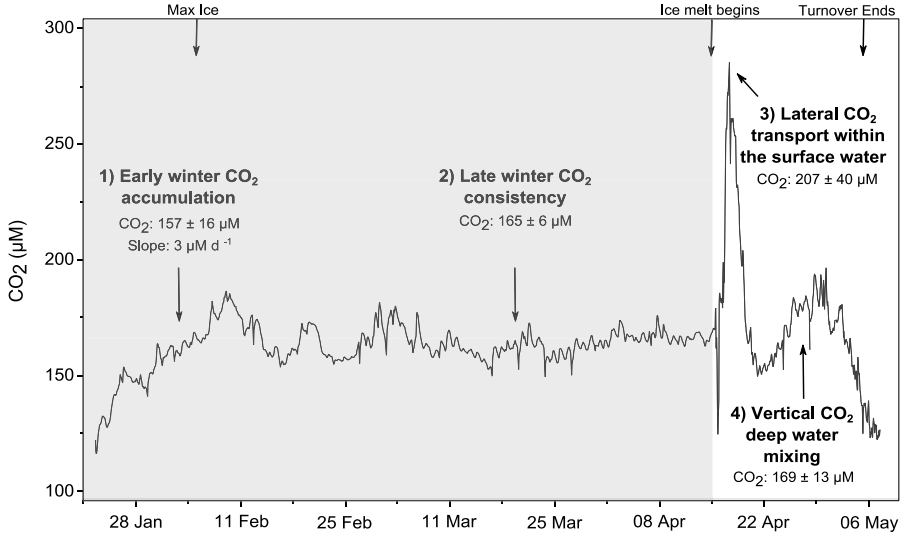

Figure 4 Automatically monitored hourly surface water (2 m) CO_2 concentrations measured over the ice cover (grey) and spring thaw period (white) above the deepest site (station site) in Lake Gäddtjärn from 22 Jan 2013–7 May 2013. For each period CO_2 mean ± standard deviation is reported. For the first period the Theil slope, indicating change over time, is reported (Figure from Denfeld et al. 2015).

Continuous CO_2 measurements from Lake Gäddtjärn resulted in two potentially distinct events of high CO_2 emission during ice-melt (Paper II). Surprisingly, the first and highest CO_2 concentration peak was likely driven by small-scale upper water column mixing of CO_2 transported laterally from the surrounding catchment. During spring thaw, snow melt-water and stream water has been shown to contain high concentrations of CO_2 (e.g. Dinsmore et al. 2011, Dinsmore et al. 2013) and since this incoming water is cold it will only mix at similar temperature gradients in the upper water column of the lake. It was not until a few days after ice-melt began, that convective turnover of deep waters became important. Although CO_2 emission rates were relatively high in the lake, rapid warming of surface waters resulted in incomplete spring lake water mixing. This resulted in 15–34 % of the wintertime accumulated CO_2 to remain in the lake, mainly in bottom waters. The fate of this reaming CO_2 is unknown, if not internally processed, the storage may only be temporary, as CO_2 may be transported downstream or emitted to the atmosphere at autumn lake water mixing.

These results indicate that some of the assumptions made in current CO_2 and CH_4 upscaling estimates may not always be true. In contradiction to the global scale CO_2 upscaling approach (e.g. Raymond et al. 2013), below ice CO_2 accumulation may not always be linear and at ice-melt incomplete lake mixing causes accumulated CO_2 to remain in the lake. Further, CO_2 and CH_4 emissions at ice-melt calculated as the difference between whole-lake CO_2 and CH_4 before and after ice-melt (e.g. Karlsson et al. 2013), may not accurately represents the actual amount of CO_2 and CH_4 emitted into the atmosphere; as stream and snow-melt water were found to source CO_2 and CH_4 into the lake during ice-melt (Paper II) and CH_4 oxidation was found to occur in temperature conditions similar to the ice-melt period (Paper III). It should be emphasized that the contribution of catchment derived CO_2 to the lake at ice-melt may be considerable, as 28–36 % of the CO_2 emission at ice-melt in Lake Gäddtjärn was estimated to be from external sources.

Although this thesis did not focus on the temporal development of CH_4 below ice, current studies suggest that CH_4 dynamics may follow similar patterns to what was found for CO_2. CH_4 accumulation is likely not linear below ice, as rates of ebullition (Walter et al. 2006) and CH_4 oxidation (Kankaala et al. 2006) may vary over the ice cover period. In some cases CH_4 accumulation below ice has been found to be low, however, high CH_4 emissions from the lake at ice-melt still persevere and have been attributed to lateral CH_4 transport from the catchment (Miettinen et al. 2014; Podgrajsek et al. 2015). In addition, incomplete water mixing has also been found to leave CH_4 accumulated in bottom waters after the ice-melt period. In a small boreal lake similar to Lake Gäddtjärn, only 54–60 % of the CH_4 accumulated during winter was released at ice melt (López Bellido et al. 2009).

Broader implications

GHG emissions from ice-covered lakes in a changing climate

In many parts of the northern hemisphere temperature increase has led to an observed change in the timing of ice-on and ice-off (Magnuson et al. 2000). Changes to ice cover duration will likely increase GHG emissions from lakes through (1) changes to hydrological connectivity in the surrounding catchment and (2) changes to thermal stability of the lake water column. Changes in the hydrology and thermal stability of lakes will lead to changes in biogeochemical cycles and hence CO_2 and CH_4 emissions from lakes into the atmosphere. The finding of this thesis, that nutrients were positively related to below ice CO_2 and CH_4 oxidation, and have previously been reported to relate to below ice CH_4 concentrations (Juutinen et al. 2009), implies that

biogeochemical cycles of C, nitrogen and phosphorus are tightly linked. Thus, changes to one element will influence the biological processes of the whole ecosystem (Chen et al. 2015). Therefore when assessing how climate and cryosphere change will effect CO_2 and CH_4 emissions from ice-covered lakes, changes to external and internal C, nitrogen and phosphorus fluxes in lakes need to be considered. Further, it is important to note that changes to C and nutrient fluxes to and within aquatic systems as a consequence of changing winter conditions likely differ across spatial scales and geographical regions (e.g. Weyhenmeyer et al. 2011; Lundin et al. 2015).

The timing of ice-on and ice-off, in combination with precipitation, modifies the mobilization of C and nutrients from the catchment to the lake via effects on runoff and vegetation (Haei and Laudon 2015). Since lateral inorganic C fluxes through the boreal watershed can sizeable (Weyhenmeyer et al. 2015), increased catchment CO_2 and CH_4 fluxes as a result of changes in climate and land use, may directly increase CO_2 and CH_4 emissions from ice-covered lakes. Further, increased DOC mobilization to lakes, in addition to nutrients, will increase in a warmer and wetter climate (Weyhenmeyer and Karlsson 2009), indirectly increasing CO_2 and CH_4 emissions. As already documented during a warmer and wetter autumn, CO_2 concentrations below lake ice were elevated (López Bellido et al. 2009). Moreover, GHG emissions from lakes located in permafrost regions are extremely sensitive to change, as in addition to changes in the hydrology and vegetation of the thawing permafrost landscape (Christensen 2004), the distribution and number of lakes will be altered (Walter et al. 2006; Tranvik et al. 2009).

The timing of ice-on and ice-off regulates the amount of energy received by the lake, subsequently affecting the seasonal thermal stability of the water column. In ice-covered lakes the thermal stability of the water column has important implications for light regimes, substrate gradients and O_2 availability, ultimately effecting bacterial activity and biogeochemical processes below ice (Bertilsson et al. 2013). In particular, the formation of deep-water anoxia plays a critical role in CH_4 production and C and nutrient cycling at the sediment-water interface. Under a changed bottom sediment redox condition additional nutrients and DOC can be released from the sediments into bottom waters (Mortimer 1941; Gonsior et al. 2013). Ice-covered lakes with low O_2 and high nutrients have resulted in high CH_4 (Juutinen et al. 2009) and CO_2 concentrations (Sobek et al. 2003, Kortelainen et al. 2006). Since an increase in winter and spring temperature will cause a reduction in the frequency and intensity of deep-water mixing (Peeters et al. 2002), favoring deep-water anoxia, an increase in CO_2 and CH_4 emissions, predominantly from bottom waters, may be expected in the future.

Future research on GHG emissions from ice-covered lakes

This thesis provides a starting point for understanding how CO_2 and CH_4 emissions from ice-covered lakes will change with a future warming and reduction to lake ice cover duration. However, the scarcity of below ice CO_2 and CH_4 data from ice-covered lakes calls for future research to better understand GHG emissions from lakes in a changing climate. Some pressing research needs that have evolved as a part of this thesis are listed below:

Improving CO_2 and CH_4 emissions from lakes: What improvements can be made to global and regional CO_2 and CH_4 emission estimates from ice-covered lakes?

Improvements to global and regional CO_2 and CH_4 emission estimates from ice-covered lakes require an understanding of processes at ice-melt; magnitude of lake water mixing, CH_4 oxidation in the water column and terrestrial CO_2 and CH_4 loading. In addition, more robust CO_2 and CH_4 emission estimates require differentiating emission potential among lake types and seasons. Although lake area has been used as a proxy for whole lake emissions (Bastviken et al. 2004;Raymond et al. 2013) and is now accessible on a global scale (Downing et al. 2006; Verpoorter et al. 2014), lake depth may be a more precise predictor (e.g. Kortelainen et al. 2006, Wik et al. 2016). However, lake depth estimates are only available for some regions (Sobek et al. 2011; Heathcote et al. 2015) and therefore more efforts should be made to accurately define lake depth on a global scale

Predicting CO_2 and CH_4 emissions from lakes in a changing climate: How will reduced lake ice cover duration alter CO_2 and CH_4 emissions from ice-covered lakes?

As the climate in northern latitudes continues to change, understanding the climate feedback of ice-covered lakes becomes increasingly important. A current study by Wik et al. (2016) used simple models to determine that CH_4 emissions from northern lakes will increase 20–54 % before the end of the century if ice-free seasons are extended 20 days. Like studies are needed to quantitatively predicate how CO_2 and CH_4 emissions from ice-covered lakes will respond to reductions in lake ice cover duration.

Dynamics at the water-ice interface: How do processes at the water-ice interface control below ice surface water CO_2 and CH_4 dynamics?

Driven by light and heat availability, biological and physical processes are dynamic at highly resolved depths just below the ice surface (Paper III; Ellis et al. 1991; Kirillin et al. 2012). Further ice-exclusion creates a concentrated

zone of DOC just below the ice (Belzile et al. 2002). The availability of light and substrate at the water-ice interface influences the interactions between microbial activity and biogeochemical processes. Yet, limited studies have focused on micro-scale processes at the water-ice interface, despite the potential significant effect on bacterial community interactions and subsequent CO_2 and CH_4 concentrations.

Linking microbiology and biogeochemistry: How does microbial activity relate to biogeochemical processes below ice?

Cross-disciplinary research that links microbial activities to biogeochemical processes is essential to understanding the response of lakes to changes in ice cover duration. For example, by linking microbial community composition to biogeochemical properties, this thesis was able to identify that a specific group of methanotrophs and subsequent CH_4 oxidation during winter was restricted to lakes with sufficient phosphate (Paper IV). More research is clearly needed on interactions between substrate availability and microbial community composition and function.

Catchment processes at ice-melt: What fraction of CO_2 and CH_4 emitted from lakes at ice-melt is derived from stream and catchment melt-water?

This thesis finds that stream and catchment melt water may significantly contribute to GHG emissions from the lake at ice-melt (Paper II). Since climate change will likely increase the mobilization of C and nutrients from the catchment to adjacent aquatic systems, understanding the current and future contribution of catchment processes to CO_2 and CH_4 emissions from lakes at ice-melt is of utmost importance. In particular, ground water contributes are seldom measured during the open water season and even less so during the ice cover period, highlighting the need for ground water measurements during the ice-cover period.

Joint effort from the scientific community: Can team-based research help answer complex scientific questions?

It is a clear outcome of this thesis that changes to lake ice cover duration will have complex consequences on GHG emissions from lakes. Fundamental to understanding complex ecosystem dynamics is research that connects micro-scale processes to broad-scale patterns. This necessitates linking experimental and modeling approaches with long term dynamics (Peters et al. 2008). Furthermore, if research is to keep up with the pace of changes to ice-covered lakes a joint effort from the scientific community is needed (Hampton and Marianne 2015).

Sensitivity to changes in lake ice cover duration: Which ecosystems are most sensitive to changes in lake ice cover duration?

Since the effects of climate change are not uniform spatially or regionally, results from this thesis suggest that the sensitivity to lake ice cover change may be greater in some areas. For instance, ecosystems along the 0˚C mean annual isotherm are extremely sensitive to changing temperatures and associated cryosphere change (Christensen 2004); as seasonally ice-covered lakes in these regions could transition to permanently open-water systems (Weyhenmeyer et al. 2011). In terms of the sensitivity of lakes to increases in GHG emissions at ice-melt, permafrost and agriculture zones, prone to major nutrient and C loss, should receive more attention. In addition, small shallow lakes are hot spots of CO_2 and CH_4 accumulation during winter (Paper I) and are important systems to monitor as they are particularly sensitive to changes in temperature and precipitation (Rautio et al. 2011).

Summary and Conclusions

The main findings of this thesis are as follows:

Spatial patterns of GHG in ice-covered lakes:

- Nutrients and lake depth are important variables in explaining below ice CO_2 and CH_4
- Below ice CO_2 and CH_4 are generally highest in small shallow lakes and bottom waters
- Below ice water column CO_2 and CH_4 are influenced by C fluxes from the catchment and lake sediment
- Surface water CH_4 concentrations are elevated near bubbles trapped at the water-ice interface, and if oxidized CO_2 concentrations may be elevated
- CH_4 oxidation is variable between lakes explained, in part, by phosphate availability and bacterial community interactions
- Below ice biogeochemical cycles of C are strongly related to phosphorus and nitrogen

Temporal patterns of GHG in ice-covered lakes:

- CO_2 and CH_4 emitted from the lake into the atmosphere at ice-melt is an important component of annual CO_2 emission estimates
- CO_2 and CH_4 accumulation below ice may not always be linear
- CO_2 and CH_4 accumulated during the ice-cover period may remain in the lake, at least temporally, if water column mixing at ice-melt is incomplete
- Stream and catchment melt water may significantly contribute to CO_2 and CH_4 emissions from the lake at ice-melt
- CH_4 oxidation near bubbles trapped at the water-ice interface has the potential to reduce CH_4 concentrations in the surrounding water prior to ice-melt

The collective findings of this thesis indicate that CO_2 and CH_4 emissions from ice-covered lakes will likely increase in the future. The strong relationship between nutrients and C processes below ice, imply that future changes to nutrient fluxes in lakes will influence the cycling of CO_2 and CH_4. Since catchment and lake sediment C fluxes play a considerable role in below ice CO_2 and CH_4 concentrations, changes to hydrology and thermal stability of lakes will undoubtedly alter CO_2 and CH_4 emissions from ice-covered lakes. Ice-covered lakes constitute a significant component of the global C cycle and will likely increase in significance with climate change. As such, ice-covered lakes should be carefully monitored and accounted for in addressing impacts of global climate change. Additional research is needed to have a more mature and complete understanding of CO_2 and CH_4 emissions from ice-covered lakes globally.

Summary in Swedish (Sammanfattning)

Kol (C) är ett vanligt förekommande grundämne på jorden och tillsammans med andra grundämnen utgör det livets byggstenar. C ingår i ett naturligt kretslopp mellan land och atmosfär. I atmosfären förekommer C i gasform som koldioxid (CO_2) och metan (CH_4). Både CO_2 och CH_4 bidrar till den naturliga växthuseffekten i jordens atmosfär. Mänsklig påverkan har ökat mängden CO_2 och CH_4 som släppts ut till atmosfären snabbare än jordens naturliga cykel vilket lett till märkbara klimatförändringar. Naturliga ekosystem som sjöar släpper också ut CO_2 och CH_4 till atmosfären. Även om sjöar utgör en liten del av jordens yta spelar de en stor roll i den globala kolcykeln. Sjöar absorberar, transporterar och använder C, vilket leder till betydande utsläpp av CO_2 och CH_4 ut till atmosfären. Som en effekt av klimatförändringarna kommer den globala cykeln av C fortsätta att förändras.

Istäckta sjöar kan vara bland de mest känsliga för klimatförändringar, och om sjöarnas istäckta period fortsätter minska i framtiden kommer stora effekter att märkas i de biogeokemiska cyklerna i dessa sjöar. Is och snö på sjöar fungerar som barriärer för fysikaliska och biologiska processer som sjöns utbyte med atmosfären, omblandning och genomträngandet av ljus i vattnet. Hur länge istäcket varar formar vattnets fysikaliska struktur och påverkar på så vis den biologiska ansamlingen av CO_2 och CH_4 under isen. Nedbrytning av organiskt material i gränsskiktet mellan sediment och vatten kan leda till höga nivåer av CO_2 och CH_4 i bottenvattnet under isen. Samtidigt kan koncentrationen av CH_4 i ytvattnet öka på grund av CH_4-bubblor som bildas i och släpps ut från sedimentet. Om CH_4 vid gränsskiktet mellan vatten och is oxideras kan koncentrationen av CO_2 också öka i ytvattnet. När isen smälter släpps CO_2 och CH_4 som har ackumulerats i sjön ut i atmosfären. Dessa utsläpp har visat sig vara en betydande del av det årliga utsläppet av CO_2 och CH_4 från sjöar. Även om istäckta sjöar är känsliga för framtida klimatförändringar finns det få studier som undersöker hur istäckets kortare varaktighet påverkar utsläppen av CO_2 och CH_4 från dessa sjöar. För att besvara dessa komplexa frågor krävs forskning som sträcker sig över flera olika skalor. Det främsta målet med denna avhandling var att fylla dessa kunskapsluckor genom att bidra med kunskap om rumslig och temporal dynamik hos CO_2 och CH_4 i istäckta sjöar.

Studierna i de fyra artiklarna baserades på olika platser: en mängd av 506 Svenska och Finska sjöar i den första artikeln, två individuella sjöar (Gäddtjärn och Erken) i den andra och tredje artikeln och sju sjöar i Upplands län i Sverige i den fjärde artikeln. Sjöarnas provtagning skedde i olika tidsintervall, från enstaka till upprepade gånger eller kontinuerligt under sjöarnas istäckta period. För varje sjö mättes växthusgaserna CO_2 och CH_4, tillsammans med mätningar av sjöns biologiska, kemiska och fysikaliska egenskaper. Med statistiska metoder bedömdes den spatiala och temporala variationen av CO_2, CH_4 och CH_4-oxidation.

Resultaten av denna avhandling visar att CO_2 och CH_4 under is varierade över rumsliga skalor mellan sjöarna. Näringsämnen var starkt kopplade till variationen av CO_2 och CH_4 under is. Regionalt, över 506 Svenska och Finska sjöar, var CO_2 under is främst kopplat till sjöns djup och näringsämnen. De observerade variationerna av CH_4-oxidation i sju istäckta sjöar kan förklaras delvis av interaktionen mellan fosfat och sjöns mikrobiella samhällen. Inom sjön påverkas även CO_2 och CH_4 under isen av C-flöden i sjösediment och från sjöns avrinningsområde, då CO_2 under isen generellt var högst i små grunda sjöar och i bottenvatten. Samtidigt fångas CH_4 bubblor som släpps ut från sjösediment till ytvattnet under isen, vilket ökar CH_4-koncentrationen i omgivande vatten och om denna CH_4 oxideras, ökar även koncentrationen av CO_2 i omgivande ytvatten.

Utöver variationerna på den rumsliga skalan varierar CO_2 och CH_4 också under sjöns istäckta tidsperiod, med oväntade variationer under perioden för issmältning. Ackumulationen av CO_2 under isen var inte linjär och vid issmältningen ledde en ofullständig omblandning av sjön till fortsatt lagring av CO_2 i bottenvattnen. Under issmältningen observerades två toppar i utsläpp av CO_2. Den första orsakades av CO_2 som transporteras från avrinningsområdet och den andra orsakades av CO_2 som transporteras upp från bottenvattnet. Detta påvisar att externa CO_2-källor kan bidra till utsläppen av CO_2 vid perioden för issmältning.

De samlade resultaten i denna avhandling påvisar att utsläpp av CO_2 och CH_4 från istäckta sjöar förmodligen kommer att öka i framtiden. Den täta kopplingen mellan näringsämnen och C-processer under isen tyder på att framtida förändringar i flöden av näring i sjöar kommer att påverka cyklerna för både CO_2 och CH_4. Då C-flöden i sjösediment och avrinningsområdet spelar en betydande roll för koncentrationen av CO_2 och CH_4 under is, kommer förändringar i sjöars hydrologi och termiska stabilitet utan tvivel påverka utsläppen av CO_2 och CH_4 från istäckta sjöar. Förändringar i utsläppen av CO_2 och CH_4 från istäckta sjöar är inte nödvändigtvis enhetlig för alla sjöar, eftersom små grunda sjöar och sjöar där jordbruk och permafrost förekommer i stor utsträckning inom avrinningsområdet kan vara bland de mest

känsliga för förändringar. Därav utgör istäckta sjöar en betydande del i den globala C-cykeln och bör noggrant bevakas i samband med framtidens klimatförändringar.

Popular Summary

Whenever I return home I am asked, what is it that you study again? And why did you have to go all the way to Sweden to study Limnology? To my friends and family back home, here is what I have been doing for the past four years: First let's start with the basics. What is Limnology? Limnology, from Greek *limne*, 'lake' and *logos*, 'knowledge', is the study of inland waters. Inland waters include lakes, ponds, reservoirs, rivers, streams, wetlands and groundwater. My research mainly focuses on lakes. So why come to Sweden to study lakes? Well for starters Sweden has over 100,000 lakes covering around 9 % of the total land area of Sweden. For a limnologist this is like being a kid at a candy store, except instead of candy the vast amount of lakes creates excitement!

Now you are probably wondering, what makes lakes so exciting? Many of us have enjoyed swimming, fishing and other recreational activities in lakes. But did you know lakes also play an important role in the global carbon cycle. Carbon is all around us, it is in the food we eat, it is in our bodies, it is in trees, it is in soils and it is in water. Like water, carbon moves between the land and the atmosphere. In a lake carbon can be stored in lake sediments, transported downstream to the ocean or released as carbon dioxide and methane into the atmosphere. When we breathe we exhale carbon dioxide. The same thing happens in a lake, when bacteria consume carbon they release carbon dioxide and methane. Both carbon dioxide and methane are greenhouse gases that absorb and retain heat in earth's atmosphere. Greenhouse gases in the atmosphere are beneficial but too much of these gases in the atmosphere can be destructive. Due to human activates, such as fossil fuel burning and agriculture, we have increased the amount of carbon dioxide and methane released into the atmosphere at a rate above that of the natural earth cycle. This increase has resulted in notable warming on earth. In Sweden, lakes are ice-covered for many months of the year. However, warming of the earth has led to a reduction in lake ice cover duration. This is where my research comes in. I am interested in understanding how reduced ice cover duration on lakes will change the amount of carbon dioxide and methane released from the lake into the atmosphere.

Let's imagine a soda can as an ice-covered lake for the time being. A closed soda contains gaseous carbon dioxide. That is why soda bubbles. Ice-

covered lakes also contain carbon dioxide in addition to methane. The ice acts similar to a lid on a soda can, keeping the gases trapped inside the lake. Part of my research investigates below ice carbon dioxide and methane dynamics in lakes. What controls the carbon dioxide and methane in an ice-covered lake? Once again the answer lies in a soda can. Soda is mainly water, sugar and carbon dioxide. The carbon dioxide in soda is forced into the can during production. This is analogous to carbon dioxide and methane entering a lake via streams and ground water. The sugar in soda is similar to organic matter in a lake. Different combinations of sugars give soda its color and flavor. The same is true for organic matter. Some lakes are brown in color like Root Beer, whereas others are clear like Spirit. Just like some people prefer to drink Root Beer over Spirit, some bacteria prefer to eat leaves over algae. Depending on what the bacteria eat and at what rate, the carbon dioxide and methane released to the water column will vary. My research suggests that both carbon dioxide and methane from streams and ground water and the consumption of organic matter in the lake contribute to below ice carbon dioxide and methane concentrations.

To take it a step further, my research tries to answer what happens to the carbon dioxide and methane in the lake at ice-melt. When you open a soda can the pressure drops and the carbon dioxide in the soda is released. This is the 'fizz' you hear when you open the can. A similar process happens at ice-melt when the 'can is opened' and the carbon dioxide and methane in the lake is released into the atmosphere. However, the rate and quantity of carbon dioxide and methane released from the lake differs depending, in part, on the water movement at ice-melt. For example, depending on the wind condition the surface water of the lake will move differently. If there is little wind and thus limited water movement on the lake, gases are slowly released from the lake. You can think of this as leaving your soda can open overnight. The next morning when you go to drink your soda it will be flat. Overnight the carbon dioxide slowly left the soda can. On the other hand if there is a lot of wind, water and gases from different depths in the lake will mix, forcing more carbon dioxide and methane to leave the lake. This is similar to shaking your soda can. By shaking the can you are forcing the carbon dioxide to be rapidly released from the soda. In the small boreal lake that I studied, I found that at the start of the ice-melt period carbon dioxide and methane were released into the atmosphere analogous to an 'open soda can'. A few days after ice-melt began the lake became a 'shaken soda can' and carbon dioxide and methane from deep waters in lake were released into the atmosphere.

So, that is what I have been doing in Sweden these past few years. I have studied the carbon cycle in ice-covered lakes. Perhaps next time you hear the 'fizz' of a soda can opening you will be reminded of my research.

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— The Little Prince by Antoine de Saint-Exupéry

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