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Carbon dynamics in highly heterotrophic subarctic thaw ponds

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Abstract

Global warming has accelerated the formation of permafrost thaw ponds in several subarctic and arctic regions. These ponds are net heterotrophic as evidenced by their greenhouse gas (GHG) supersaturation levels (CO_2 and CH_4), and generally receive large terrestrial carbon inputs from the thawing and eroding permafrost. We measured seasonal and vertical variations in the concentration and type of dissolved organic matter (DOM) in five subarctic thaw (thermokarst) ponds in northern Quebec, and explored how environmental gradients influenced heterotrophic and phototrophic biomass and productivity. Late winter DOM had low aromaticity indicating reduced inputs of terrestrial carbon, while the high concentration of dissolved organic carbon (DOC) suggests that some production of non-chromophoric dissolved compounds by the microbial food web took place under the ice cover. Summer DOM had a strong terrestrial signature, but was also characterized with significant inputs of algal-derived carbon, especially at the pond surface. During late winter, bacterial production was low (maximum of 0.8 mg C m^{-3} d^{-1}) and was largely based on free-living bacterioplankton (58 %). Bacterial production in summer was high (up to 58 mg C m^{-3} d^{-1}), dominated by particle-attached bacteria (67 %), and strongly correlated to the amount of terrestrial carbon. Primary production was restricted to summer surface waters due to strong light limitation deeper in the water column or in winter. The phototrophic biomass was equal to the heterotrophic biomass, but as the algae were mostly composed of mixotrophic species, most probably they used bacteria rather than solar energy in such shaded ponds. According to the $\delta^{13}C$ analyses, non-algal carbon supported 51 % of winter and 37 % of summer biomass of the phantom midge larvae, *Chaoborus* sp., that are at the top of the trophic chain. Our results point to a strong heterotrophic energy pathway in these thaw pond ecosystems, where bacterioplankton dominates the production of new carbon in both summer and winter.

1 Introduction

Traditional view of inland waters as sinks of carbon has changed during the past decades, and at present, lakes and ponds are considered net sources of carbon to the atmosphere (Tranvik et al., 2009). Increasing attention has been given to thaw ponds and lakes after recognizing the cumulative effect of their high abundance and greenhouse gas (GHG) emissions on global warming (Kling et al., 1992; Hamilton et al., 1994; Nakano et al., 2000; Walter et al., 2006; Desyatkin et al., 2009; Laurion et al., 2010), especially when they emit old carbon thus having the potential to act as a positive feedback mechanism on climate (Anthony et al., 2014). Thaw ponds and lakes are dominant in continuous and discontinuous permafrost areas, for example in permafrost regions of Siberia where they represent 90 % of all lakes (Walter et al., 2006), but until recently, little has been known on the limnological properties and microbial communities of this important freshwater ecosystem (Breton et al., 2009; Tank et al., 2009; Negandhi et al., 2013, 2014; Rossi et al., 2013; Sepulveda-Jauregui et al., 2014).

Subarctic thaw ponds can be highly turbid and have relatively high nutrient concentrations (Breton et al., 2009; Rautio et al., 2011a) compared to most high latitude freshwater ecosystems (Pienitz et al., 1997; Hamilton et al., 2001; Medeiros et al., 2012). Moreover, high perimeter/volume ratio, the presence of palsas and bogs and the thawing of organic-rich permafrost in their watershed favor high inputs of dissolved organic matter (DOM) to the ponds. The rate of DOM input to aquatic systems has increased over the last decades as a result of warmer temperatures (Hudson et al., 2003), and the recent mobilization of terrestrial carbon stocks stored for thousands of years in the permafrost (Vonk et al., 2012) Chromophoric DOM (CDOM) can influence water column temperature regimes through its absorption of sunlight (Caplanne and Laurion, 2008), and with suspended particles, they contribute to form a distinct and stabile thermocline and strongly regulate the depth of the euphotic zone (Watanabe et al., 2011). Light is limited usually to the first meter, therefore restricting the water volume where photosynthesis can occur. This type of environment favors heterotrophic

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bacterial production (BP) that was shown to reach similar rates as in eutrophic lakes (Breton et al., 2009). The limnological characteristics of thaw ponds are likely also beneficial to mixotrophic algae and heterotrophic protozoans, as flagellated species are generally well adapted when lakes are rich in humic compounds (Jones, 2000). In low light conditions they can utilize bacteria as an energy source, and as they are motile they also benefit from the nutrient-rich bottom waters (Arvola et al., 1991). They have been shown to be a key link in the carbon transfer from low to high trophic levels in small boreal forest lakes (Salonen and Rosenberg, 2000).

Bacterial metabolism on allochthonous carbon determines its transfer to mixotrophic algae and heterotrophic protozoans, to zooplankton feeding on bacteria, and via predation to higher trophic levels. Many recent studies consider terrestrially-derived carbon as an important source of energy for aquatic bacteria, especially when algal production is limited, and a subsidy to higher trophic levels despite its lower quality (Jansson et al., 2000; Cole et al., 2006; Berggren et al., 2010). Before entering aquatic ecosystems, DOM has already been degraded and transformed by soil microbes (Wetzel, 1995; Kalbitz et al., 2003), and contains mainly the recalcitrant fraction of this carbon pool and no essential fatty acids required by all organisms (Brett et al., 2009, 2012). However, carbon budgets performed on an increasing number of lakes, taking into account the carbon flow from soils to lakes, and its transformation and transport to the atmosphere and to sediment storage, suggest that an important part of soil carbon is metabolized in lakes (Cole et al., 2007; Tranvik et al., 2009). Part of this metabolization is made possible through the action of sunlight in lake water, which transforms DOM into smaller, more labile molecules (Lindell et al., 1995; Laurion and Mladenov, 2013).

Circumpolar thaw ponds are ice covered for a large fraction of the year, which further affects carbon cycling, and generates large seasonal variations. In the absence of light, autotrophic productivity stops while respiration continues, resulting in high GHG releases in spring (Striegl et al., 2001). The thermal stratification in summer also acts as a barrier and creates another habitat where GHG and organic carbon accumulate, leading to GHG storage flux during the autumnal overturn. The ponds can also be disconnected or poorly connected to a hydrographic network (Bouchard et al., 2011), affecting carbon cycling influenced mainly by evaporation and sedimentation. Hence the dissolved inorganic and organic carbon pools in subarctic thaw ponds may vary widely in time and space. The aim of this study was to demonstrate this variability, and to show how it influences GHG accumulation, CDOM characteristics, and autotrophic and heterotrophic carbon pools. Comparisons were made between late winter and summer, and between surface and bottom waters in summer. We also make an attempt to estimate the role of terrestrial carbon in the diet of higher organisms in the ponds. This study follows earlier ones looking at the limnological characteristics and bacterial communities of these subarctic thaw ponds in summer (Breton et al., 2009; Negandhi et al., 2013, 2014; Rossi et al., 2013).

2 Methods

2.1 Sample collection and limnological analyses

The study was carried out in the discontinuous permafrost region near the village of Whapmagoostui-Kuujjuarapik (55°20′ N, 77°30′ W) along the River Kwakwatanikapistikw (local Cree name; KWK is used to name the ponds hereafter) where a large number of thaw ponds can be found. At this site, ponds are thermokarstic and form over an impermeable clay-silt bed, preventing most hydrological interactions among ponds, on center of thawed lithalsas (or inorganic palsas). They are surrounded by dense shrubs and sparse trees, and occasional areas of mosses and aquatic plants. More details on the study area are provided in Bouchard et al. (2014, 2011).

Five ponds were studied during late winter (06–11 April) and summer (08–14 August) in 2009. They are all small (averaged diameter 17 ± 1.3 m) and shallow (average depth 2.5 ± 0.4 m). Sampling was done with a Kemmerer water sampler (Wildco® USA) through a borehole drilled into the ice in winter, and from an inflatable boat in summer at the middle of the pond. During winter sampling, the water started pouring over the ice through the hole because of the pressure from the weight of snow and ice, and possibly resulting in a mixing of surface with deeper water. This was suggested as the factor explaining the similar GHG concentrations obtained in surface and bottom waters, despite the expected inverse thermal stratification at this period of the year (Laurion et al., 2010). All other samples were collected from about 1 m below the ice and considered as representative of an integrated water column. In summer, surface and bottom waters were sampled from just below the surface and approximately 0.5 m above the bottom sediments.

Measures of temperature, dissolved oxygen, pH and conductivity were done with a 600R YSI multiparametric probe (Yellow Springs Inc.). Further analyses were performed on water prefiltered through a 50 µm sieve. Total suspended solids (TSS) were obtained by filtering 500–1000 mL of water onto precombusted and preweighted GF/F filters (Advantec MFS Inc.). The 50 µm prefiltration reduced the TSS by an average 5.8 % in comparison to bulk water samples, both analyzed in summer (data not shown). Filters were stored at −20 °C until they were dried for 24 h at 60 °C, and weighted to get sestonic dry weight or TSS. They were subsequently combusted at 450 °C for 2 h to estimate the organic fraction of TSS and to be able to calculate the organic fraction of TSS. An aliquot of water was filtered through a pre-rinsed cellulose acetate filter (0.2 µm pore size; Advantec MFS Inc.) to analyse soluble reactive phosphorus (SRP; unpreserved samples) and iron (Fe; samples preserved with HNO_3 at 0.15 % final concentration). Total phosphorus (TP) and total nitrogen (TN) were analysed from unfiltered water preserved with H_2SO_4 (final concentration of 0.15 %). All nutrient samples were stored in acid-washed glass bottles in dark and cold (4 °C) until further analysis as in Breton et al. (2009).

2.2 Carbon characterization

Dissolved CO_2 and CH_4 were determined as in Laurion et al. (2010). In brief, 2 L of pond water were equilibrated into 20 mL of ambient air for 3 min, with the headspace sampled in duplicated glass vials (Vacutainers©) previously flushed with helium and vacuumed. Gas samples were analyzed by gas chromatography (Varian 3800), and dissolved gas concentrations were calculated according to Henry's Law.

The water filtered through pre-rinsed cellulose acetate filters as above was also used to analyze dissolved organic carbon concentration (DOC), and for optical analyses of CDOM. Samples were stored in amber glass bottles in dark and cold (4 °C) until the analysis. DOC was quantified using a carbon analyzer (Shimadzu TOC-5000A) calibrated with potassium biphthalate. The absorbance was measured from 200 to 800 nm with a spectrophotometer (Varian Cary 300), using 1 cm quartz cuvettes on dual-beam mode, at 1 nm intervals for winter samples, and 4 nm intervals for summer samples. Null-point adjustment was performed using the mean value from 750–800 nm, and the absorption coefficients (a_λ) were calculated from absorbance measurements (A_λ) at 254 and 320 nm using $a_\lambda = 2.303\ A_\lambda / L^{-1}$, where L is the length of the cuvette in meters (Mitchell et al., 2002). The absorption coefficient at 320 nm (a_{320}) was used as an index of CDOM concentration. Specific UV absorbance–index (SUVA$_{254}$) was determined from DOC normalized A_{254}, and used as an index of aromaticity (Weishaar et al., 2003).

CDOM absorption spectra were further analyzed to calculate the spectral slopes S_λ (Loiselle et al., 2009) between 250 and 450 nm (Galgani et al., 2011). Slopes were calculated over 20 nm intervals with a 1 nm step (i.e. 250–269, 251–270,...) for winter samples, and 4 nm steps for summer samples (i.e. 250–269, 254–273,...). The resulting set of spectral slopes was plotted by center wavelengths. Calculations were performed in open source software package SciLab 4.15. The individual spectral slope S_{289} was used to evaluate the amount of fulvic and humic acids likely related to the autochthonous production (Loiselle et al., 2009). Algal-derived carbon has a maximum slope at 289 nm, while terrestrial carbon spectral slopes lack this peak and present a spectrally variable distribution with a steady increase from 260 to 390 nm.

2.3 Microbial abundance and productivity

For the determination of chlorophyll *a* (Chl *a*) concentrations, 1–2 L of 50 µm-sieved pond water were filtered onto GF/F filters. Samples were collected in duplicates and stored at −80 °C until pigment extraction and fluorometric analysis were done in hot ethanol according to Nush (1980). Water samples for the enumeration of nanoflagellates (PNF: phototrophic and mixotrophic cells; HNF: heterotrophic cells) and phototrophic picoplankton (PPA) were preserved with 0.2 µm-filtered glutaraldehyde solution at a final concentration of 1 %. Three replicate aliquots (3–5 mL) were filtered through 0.6 µm black polycarbonate filters (Nuclepore). Samples were stained with 4-,6-diamido-2-phenylindole (DAPI), mounted to slides and stored at −20 °C until counting under UV excitation with an epifluorescense microscope (Zeiss Axiovert 200) at 1000× magnification. Discrimination between pigmented and heterotrophic nanoflagellates was done with green excitation light. At least 50 cells or a maximum of 30 fields were counted from each sample. Nanoflagellate cells were further divided into three size categories: < 5, 5–10 and > 10 µm. Volumes were converted to carbon biomass using the carbon content coefficient of $0.19\,\mathrm{pg\,C\,\mu m^{-3}}$ for PNF and HNF (Putt and Stoecker, 1989). Phototrophic picoplankton carbon content was calculated using the carbon conversion equation ($\mathrm{pg\,C} = 0.433 \times V^{0.866}$, where V is in μm^3) for picoeukaryotic cells (Verity et al., 1992; Campbell et al., 1994).

Bacterial abundance (BA) was measured with a flow cytometer (FACSCalibur, Becton-Dickinson) as in Rossi et al. (2013) before and after sonication to obtain estimations of free-living and particle-attached bacterial abundance. Biomass calculation for bacterioplankton was based on biovolumes measured from digital images acquired from DAPI-stained microscope slides using the *Cell C* program (Selinummi et al., 2005). Average bacterial carbon content was first estimated with allometric conversion formula recommended for DAPI stained cells ($\mathrm{fg\,C} = 218 \times V^{0.86}$, where V is in μm^3) (Posch et al., 2001). The average cellular carbon content ($18.1\,\mathrm{fg\,C\,cell^{-1}}$) was then multiplied by the bacterial abundance.

Bacterial production was measured from unfiltered and filtered (3 µm) water samples using tritiated leucine (^{3}H-leucine) incorporation with centrifugation (Smith and Azam, 1992). A solution of ^{3}H-leucine (specific activity of 164 Ci mmol^{-1}) was added to each vial to obtain a final leucine concentration of 30 nM, at which bacteria were saturated (experimentally tested). During the winter, the samples were incubated at ∼ 0 °C in the dark for 2 h. During the summer, samples were incubated at in situ temperatures (5–18 °C), depending on ponds. BP was stopped by adding trichloroacetic acid (5 % final concentration), and samples were then stored at −20 °C before the centrifugation step. Winter samples were radioassayed with a Perkin Elmer Tri-Carb 2800, and summer samples with a Beckman LS 6500. Leucine incorporation was converted to carbon biomass using coefficients from Simon and Azam (1989). Bacterial respiration (BR) was estimated from BP according to Del Giorgio and Cole (1998) BR model II.

Primary production (PP) was measured from the mixed water column during winter and from the surface in summer. An incubation system generating a gradient of photosynthetically active radiation (PAR), introduced by Rae and Vincent (1998), was used to obtain photosynthesis vs. irradiance curves from complete darkness to full sunlight ($E_{\max}$). The value for $E_{\max}$ was calculated from in situ PAR measurements available from a weather station located in Whapmagoostui-Kuujjuarapik, and assuming the air-water surface in these humic waters to cause a 50 % decrease in radiation levels (Doxaran et al., 2004). A water volume of 20 mL was inoculated with a working solution of [^{14}C]-HCO_3 (80 µCi mL^{-1}) to a final concentration of 0.2 µCi mL^{-1}. In winter, the incubations were done outside (∼ 0 °C) under natural light conditions in a water bath for 45–60 min, while in summer a circulating water bath was used to keep samples at in situ temperature (14–18 °C) and incubations were run for 120 min. The incubations were terminated by filtrating samples onto GF/F filters, and subsequently frozen before they were radioassayed with a Perkin Elmer Tri-Carb 2800 liquid scintillation counter. Chl *a* normalized carbon fixation rates were fitted to the equation of Platt et al. (1980) or Jassby and Platt (1976) depending on the presence or absence of photoinhibition, respectively. Data fit to the equations had on average a r^2 value of 0.92, and always higher than 0.81. The iterative non-linear regression of SigmaPlot 11.0 was used to obtain the maximum photosynthetic rate (P_{max}). PP at the pond bottom was estimated from the photosynthesis-irradiance curves and PAR estimated from the diffuse attenuation coefficients calculated from a linear regression using TSS and DOC (Watanabe et al., 2011). Without light under the ice and snow cover (measured), PP was established at zero.

2.4 Carbon assimilation in the food web

Trophic transfer of carbon through the food web was evaluated with δ^{13}C stable isotopes. The role of different carbon sources for phantom midge larvae (*Chaoborus* sp.) was calculated using δ^{13}C end-member values of phytoplankton and terrestrial carbon. *Chaoborus* is at the top of the food chain in these fishless ponds. The phytoplankton δ^{13}C signature was considered a function of the $\delta^{13}CO_2$ signature and the photosynthetic fractionation parameter (ϵ_p):

$$\delta^{13}C_{algae} = \delta^{13}CO_{2(aq)} - \epsilon_p$$

$\delta^{13}CO_2$ was obtained from the analyses run for the summer surface waters (G.G. Hatch Stable Isotope Laboratory, University of Ottawa, Canada). ϵ_p was calculated from the linear relationship between ϵ_p and phytoplankton growth rate divided by the measured CO_2 concentration (μ/CO_2), as described by Laws et al. (1995), where $\epsilon_p = ((\mu/CO_2) - 0.371)/-0.015$. Phytoplankton growth rate (μ) was estimated as the ratio between algal biomass and PP (Table A1). Algal biomass was calculated from Chl *a* concentration by using a carbon : Chl *a* conversion factor of 42.4 of unfed low light-adapted mixotrophic dinoflagellates (Skovgaard et al., 2000). This factor was chosen because mixotrophic species are by far the most abundant group in these ponds, (Dupont, 2008; Forsström, unpublished data). Normally there are large variations in the C : Chl *a* ratios (Moal et al., 1987) and therefore $\delta^{13}C_{algae}$ calculations were tested for C : Chl *a* ratios from 25 to 100. $\delta^{13}C_{algae}$ was not significantly impacted by ratio change.

An average δ^{13}C signature of −28.21 ‰ ± 0.15 obtained from the boreal region (Marshall et al., 2007) was used as the terrestrial carbon end member.

Chaoborus population was sampled with 50 µm plankton net, three replicates each approximately 10 individuals were freeze-dried and grinded to a fine powder before stable isotope analysis. POM samples that were considered as food source for *chaoborus* were collected by filtering up to 2 L of water through precombusted GF/F filters. The filters were freeze-dried and the organic layer was removed for stable isotope analyses that were performed with a Carlo Erba Flash EA1112 elemental analyzer connected to a Thermo Finnigan DELTA$^{\text{plus}}$ Advantage CF-IRMS. Three replicates were analyzed from each sample. Pike (*Esox lucius* L.) white muscle tissue was used as an internal laboratory working standard, calibrated against International Atomic Energy Agency standards. Internal precision was always better than 0.2 ‰.

2.5 Data analysis

Correlations between organisms (abundance, biomass and productivity measurements) and environmental variables were tested with non-parametric Spearman's rank correlation coefficient analysis (IBM SPSS statistic 20.0). Environmental variables are illustrated with a principal component analysis (PCA) in Fig. 4 (PAST version 2.17c), where biological variables were entered as vectors which length and direction were determined by Spearman's correlation analysis between biological variables and PCA axis 1 and 2. The contribution of carbon from phytoplankton and terrestrial sources to the *Chaoborus* diet was calculated using the linear IsoError mixing model which partitions two sources with a single isotopic signature (e.g., δ^{13}C).

3 Results

3.1 Physicochemical properties of thaw ponds

In late winter, the ponds were covered with 50 to 70 cm of snow and approximately 30 to 60 cm of ice, which absorbed all light. Water temperature was 2.0 °C under the ice and the ponds were likely O_2 depleted at the bottom because of the smell of hydrogen sulfide, while O_2 concentration was $4.5 \pm 3.5\,\mathrm{mg\,L^{-1}}$ in the integrated water column sample. In summer, despite their shallow depth, ponds are strongly stratified with nearly 10 °C difference in temperature and $10\,\mathrm{mg\,L^{-1}}$ difference in O_2 between surface and bottom (Fig. 1). The thermocline was situated at 1.6 ± 0.4 m. The pH varied between 6.0 and 7.5, with lowest and highest values respectively measured in summer bottom and surface waters. There was no difference in conductivity between winter ($50 \pm 7\,\mathrm{\mu S\,cm^{-1}}$) and summer at the surface ($46 \pm 10\,\mathrm{\mu S\,cm^{-1}}$) but measured values from bottom waters ($194 \pm 67\,\mathrm{\mu S\,cm^{-1}}$) were higher. Nutrients were relatively high in all samples. TN concentrations were elevated in winter ($958 \pm 235\,\mathrm{\mu g\,N\,L^{-1}}$) compared to the summer values ($264 \pm 118\,\mathrm{\mu g\,N\,L^{-1}}$). TP was relatively high in winter ($97 \pm 43\,\mathrm{\mu g\,P\,L^{-1}}$), and in summer the concentrations were clearly lower at the surface ($55 \pm 29\,\mathrm{\mu g\,P\,L^{-1}}$) than at the bottom ($3110 \pm 1043\,\mathrm{\mu g\,P\,L^{-1}}$). SRP was available during the whole year, with the highest concentrations observed in late winter ($26 \pm 15\,\mathrm{\mu g\,P\,L^{-1}}$) and in summer bottom waters ($31 \pm 36\,\mathrm{\mu g\,P\,L^{-1}}$), but surface concentrations in summer were relatively low ($3.1 \pm 3.0\,\mathrm{\mu g\,P\,L^{-1}}$). All ponds had higher TSS in bottom waters ($85 \pm 43\,\mathrm{mg\,L^{-1}}$), while in winter and summer surface waters the concentrations were generally an order of magnitude lower. In most ponds, organic fraction of TSS followed the same trend as TSS and made on average 24 % of TSS. Fe was lower at the surface ($0.3 \pm 0.1\,\mathrm{mg\,L^{-1}}$) than at the bottom of ponds ($3.1 \pm 1.6\,\mathrm{mg\,L^{-1}}$) in summer. No Fe measurements were done during late winter. Limnological properties of the ponds are summarized in Table 1.

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3.2 Carbon characterization

CO_2 and CH_4 concentrations were high in winter (up to 357 and 14.1 µM respectively), and particularly high at the pond bottom in summer (up to 815 and 312 respectively; Table 2). Surface waters, in contact with the atmosphere, had one order of magnitude lower concentrations, but values remained supersaturated. DOC ranged from 4.1 to 10.5 $\text{mg}\,\text{L}^{-1}$, with the highest concentrations obtained in winter. Despite the higher DOC observed in winter, CDOM was lowest at this period, as indicated by a_{320} values ($7.1 \pm 2.5\,\text{m}^{-1}$ compared to 27 ± 10 and $70 \pm 37\,\text{m}^{-1}$ at the surface and bottom in summer, respectively). SUVA_{254} followed the same trend as a_{320}, with lower values in winter ($0.8 \pm 0.2\,\text{L}\,\text{mg}\,\text{C}^{-1}\,\text{m}^{-1}$) compared to summer surface ($4.8 \pm 1.0\,\text{L}\,\text{mg}\,\text{C}^{-1}\,\text{m}^{-1}$) and bottom waters ($7.7 \pm 2.4\,\text{L}\,\text{mg}\,\text{C}^{-1}\,\text{m}^{-1}$), indicating the presence of more aromatic compounds, and possibly DOM-Fe complexes. The shape of absorption spectral slopes showed a clear maximum at 382 nm, indicating the presence of terrestrial fulvic and humic acids. Consistent with the SUVA_{254} index, S_{382} values were relatively low in winter (except in pond KWK2) ($0.0137 \pm 0.0016\,\text{nm}^{-1}$), while they were clearly higher in summer surface waters ($0.0158 \pm 0.0014\,\text{mg}\,\text{nm}^{-1}$), and especially in bottom waters ($0.0169 \pm 0.0007\,\text{nm}^{-1}$). The individual spectral slope S_{289} indicates that higher amounts of algal-derived carbon were present in summer surface waters ($0.0148 \pm 0.0009\,\text{nm}^{-1}$), especially in the most transparent pond KWK6 ($0.0162\,\text{nm}^{-1}$), while their role was limited in the dark habitats under the ice ($0.0113 \pm 0.0011\,\text{nm}^{-1}$) and in bottom waters ($0.0112 \pm 0.0007\,\text{nm}^{-1}$). Carbon quantity and CDOM quality properties are summarized in Table 2, and the seasonal differences in absorption spectral slopes are shown in Fig. 2.

3.3 Microbial abundance and productivity

The abundance of all organisms examined was highest in the summer bottom waters, but the magnitude and seasonal distribution differed among taxa and ponds (Table 3). Especially, the abundant motile PNF accumulated in the nutrient-rich bottom waters, where their abundance was in most ponds an order of magnitude higher than at the surface (110 ± 89 vs. $27 \pm 8 \times 10^6\,L^{-1}$). The less abundant HNF also favored the bottom waters, with an order of magnitude difference in the abundance between bottom and surface waters (9.2 ± 11.6 vs. $0.8 \pm 0.7 \times 10^6\,L^{-1}$). The smaller phototrophic picoplankton (PPA) and bacteria were more uniformly distributed, although in most ponds the abundances were slightly higher at the bottom. Abundance was also quantified for free-living and particle-attached bacteria. During late winter, 74 ± 9 % of bacterioplankton was attached to particles, and 46 ± 21 % and 70 ± 17 % in summer surface and bottom waters (Table B1).

When converted to biomass, the seasonal and vertical distribution pattern was even more accentuated (Table 3, Fig. 3). Overall, lower biomasses were encountered in winter, and higher at the bottom of the water column in summer. Total phototrophic biomass as Chl *a* concentration ($5.6 \pm 2.5\,\mu g\,L^{-1}$) as well as the PNF biomass ($152 \pm 68\,\mu g\,C\,L^{-1}$) under the ice were relatively high. Summer surface phototrophic biomass was similar to winter biomass, and it was highest in the dark bottom waters, likely reflecting cell sedimentation. The biomass of strictly phototrophic PPA was very low in winter ($5.8 \pm 4.4\,\mu g\,C\,L^{-1}$) and an order of magnitude higher in summer. The bacterial biomass was always high when compared to literature, although samples differed significantly from each other, with the lowest biomass occurring in winter ($109 \pm 67\,\mu g\,C\,L^{-1}$), two times higher biomass in summer at the surface ($223 \pm 36\,\mu g\,C\,L^{-1}$), and five times higher at the bottom ($520 \pm 146\,\mu g\,C\,L^{-1}$). The HNF contributed little to the total microbial biomass, especially in the illuminated summer surface waters where they averaged $3.2 \pm 2.9\,\mu g\,C\,L^{-1}$. Their biomass was higher at the bottom ($39.2 \pm 49.4\,\mu g\,C\,L^{-1}$) and in winter samples ($8.9 \pm 4.7\,\mu g\,C\,L^{-1}$).

Snow and ice cover prevented light penetration under the ice, and therefore we assumed that no PP occurred in situ in late winter. However, the photosynthetic capacity of late winter phytoplankton community was not null, and represents the potential at the ice-out, which took place 2–3 weeks later. The maximum photosynthetic rate (P_{max}) of late winter phytoplankton community was for most ponds an order of magnitude lower than $P_{\max}$ of the summer community (2.0 ± 2.1 vs. $30.6 \pm 26.1\,\mathrm{mg\,C\,m^{-3}\,d^{-1}}$). BP rates were very low in winter ($0.4 \pm 0.2\,\mathrm{mg\,C\,m^{-3}\,d^{-1}}$) compared to the summer when surface ($31 \pm 14\,\mathrm{mg\,C\,m^{-3}\,d^{-1}}$) and bottom ($42 \pm 19\,\mathrm{mg\,C\,m^{-3}\,d^{-1}}$) BP rates were similarly high. BR rates calculated from BP were low in winter ($2.0 \pm 0.6\,\mathrm{mg\,C\,m^{-3}\,d^{-1}}$) and equally high during summer in surface ($28 \pm 6\,\mathrm{mg\,C\,m^{-3}\,d^{-1}}$) and in bottom ($33 \pm 6\,\mathrm{mg\,C\,m^{-3}\,d^{-1}}$). Particle-attached bacterioplankton played an important role in pond production at both sampling seasons (late winter: 42±20 %; summer surface: 66±20 %; bottom: 68±44 %; Table B1).

Winter, surface and bottom environmental characteristics formed three distinct groups on the PCA (Fig. 4a), with the first two axes explaining 72.9 % of the variation in the environmental variables (PC1 46.0 % and PC2 26.9 %). Axis PC1 has strong positive correlations with TP ($r = 0.91$), a_{320} ($r = 0.80$), TSS ($r = 0.83$) and GHG (CO_2 ($r = 0.92$) and CH_4 ($r = 0.90$)), and strong negative correlations with pH ($r = -0.81$) and S_{289} ($r = -0.65$), whereas PC2 has positive correlation with temperature ($r = 0.81$), S_{382} ($r = 0.69$) and SUVA_{254} ($r = 0.76$), and negative correlation with TN ($r = -0.93$) and DOC ($r = -0.67$). Phototrophs (PP, PNF and PPA) were more strongly correlated to PC2 and its associated nutrients and DOC, while heterotrophs (bacteria biomass; BB and HNF) were correlated with PC1 and its associated carbon quality indices (Fig. 4b, Table 4).

3.4 Carbon assimilation

The variability in mean *Chaoborus* δ^{13}C values between winter (−34.1 ‰) and summer (−34.3 ‰) was small (Fig. 5a). Phytoplankton δ^{13}C values ranged between −34.3 and −41.4 ‰ in different ponds (Table B1). The values of POM fell between the terrestrial and algal end-member values reflecting the presence of both types of carbon in the water column (Fig. 5a). According to the mixing model, on average 42 % of *Chaoborus* carbon diet came from terrestrial sources in winter, while in summer the terrestrial share was 10 % smaller for most ponds, thus *Chaoborus* diet became clearly dominated by algal sources (Fig. 5b). Only in one pond (KWK6) terrestrial carbon contributed substantially (70 %) to the *Chaoborus* diet.

4 Discussion

The large variations in physicochemical characteristics of thaw ponds over the seasons and down the water column were reflected in their ecological properties. The cold and nutrient-rich winter waters had the lowest microbial abundance and productivity. The warm and illuminated summer surface waters favored primary production, while the colder and darker bottom waters accumulated nutrients, carbon compounds and microorganisms. The overall supersaturation in GHG and the clear dominance of heterotrophy over phototrophy indicate that the majority of the energy was flowing through the heterotrophic food web.

4.1 Spatial and seasonal variations in GHG

Greenhouse gas storage in pond waters occurred in winter under the ice cover and in summer under the steep thermocline, due to the isolation of these water masses from atmospheric venting. Partial pressures measured were especially large in summer hypolimnetic waters (in average 13 674 µatm of CO_2 and 4783 µatm of CH_4) compared to values at the surface (in average 1206 µatm of CO_2 and 9 µatm of CH_4). Such heterogeneity in the vertical distribution of GHG is typical for seasonally stratified lakes where bottom values are often many folds higher than at the surface (Eller et al., 2005; Guérin et al., 2006; Bastviken et al., 2008). Partial pressures of CO_2 at the surface of thaw ponds (598–1545 µatm) were comparable to values obtained in other regions, for example in European boreal lakes (990 µatm; Kortelainen et al., 2006), Canadian boreal streams and rivers (1850 µatm; Teodoru et al., 2009), Western Siberian lakes and ponds (1935 µatm; Shirokova et al., 2012), or Canadian subarctic and arctic ponds (1896 µatm; Breton et al., 2009). Surface water CH_4 partial pressures (6–13 µatm) were also in the same range as values reported in lakes and ponds from North-America (11–59 µatm; Bastviken et al., 2008), Finland (23 µatm; Juutinen et al., 2009), Canadian Subarctic and Arctic (22 µatm; Breton et al., 2009), and Western Siberia (30 µatm; Shirokova et al., 2012).

The dominance of BR over PP, combined with the isolation of water masses during the long winter, followed by a very short spring mixing period (Laurion et al., 2010) and the steep summer stratification of these ecosystems controlled the accumulation of GHG in the hypolimnion. When normalized by the duration of the isolation period, GHG accumulated more rapidly in summer at the pond bottom ($6.8 \pm 2.2\,\mu M\,CO_2\,d^{-1}$ and $1.9 \pm 0.9\,\mu M\,CH_4\,d^{-1}$) than in winter under the ice cover ($1.5 \pm 0.3\,\mu M\,CO_2\,d^{-1}$ and $0.030 \pm 0.027\,\mu M\,CH_4\,d^{-1}$). This may be partly due to the more abundant microbial community in summer, although most GHG produced likely came from benthic respiration, especially in such shallow systems (Kortelainen et al., 2006). Summer also provides fresh organic matter that may stimulate GHG producers that indeed presented higher respiration rates. The smaller CH_4 accumulation rates in winter might also result from more optimal conditions for methanotrophy under the ice cover where bubbling CH_4 is trapped and dissolves in water. The amount of CH_4 in a lake was shown to depend on the size of the anoxic layer (Fendinger et al., 1992; Bastviken et al., 2004), and in the present study, this layer represents a particularly large proportion of the water volume in summer. During the autumnal turnover period (lasting about 2 months), the whole water column becomes oxygenated, and in the first part of the winter surface layer of the pond may contain sufficient oxygen (Deshpande et al., 2015) for efficient CH_4 consumption. Anoxic methanotrophy has also been reported (Sivan et al., 2011) and may occur at our study sites. Nevertheless, these GHG storage periods indicate that subarctic thaw ponds will release large amounts of CH_4 during the autumnal mixing period, and also during spring turnover if it lasts long enough (Walter et al., 2006; Laurion et al., 2010).

4.2 Seasonality in CDOM properties

We used a_{320} as an indicator of the quantity of CDOM, and SUVA$_{254}$, S_{289} and S_{382} as indicators of the aromatic content of CDOM and the relative proportions in allochthonous (terrestrial) vs. autochthonous (algal) carbon sources. The high a_{320} and SUVA$_{254}$ values indicate a large contribution by terrestrial humic substances in DOM at the surface of thaw ponds in summer, with values similar to a few years earlier in the same ponds (Breton et al., 2009; Watanabe et al., 2011). CDOM clearly decreased along the winter (late winter a_{320}; Table 2) and became less aromatic (SUVA$_{254}$). The high DOC values in winter (average of 8.3 mg L^{-1} compared to 5.8 mg L^{-1} in summer surface) but its low aromaticity suggests that carbohydrates or protein-like compounds made up a larger fraction of DOM in winter, resulting from an interruption of allochthonous inputs, and a larger contribution by bacteria-induced CDOM-degradation under the ice. Laurion et al. (unpublished data) tested the role of bacterial CDOM degradation in arctic thaw ponds and found that its importance can almost match that of photodegradation in certain cases, without significant losses in DOC, potentially indicating a bacterial transformation into less colored compounds. Although BP in late winter was low, the long subarctic winters allow accumulation effects that could lead to a decrease in CDOM. The labile part of DOC is known to be consumed within days by bacterioplankton, leaving the recalcitrant fraction of DOC to dominate in environments where fresh inputs are limited (Del Giorgio and Davis, 2002; Roehm et al., 2009; Guillemette and del Giorgio, 2011). However this is not clearly observed in the present study thaw ponds, where less aromatic and non-chromophoric fractions increased along winter, likely as the result of DOM recycling by a rich microbial food web, together with a lack of new carbon inputs from the frozen catchment.

The high a_{320} and SUVA$_{254}$ values found in bottom waters are very likely caused by the elevated dissolved iron concentrations (up to 5.1 mg L^{-1}; $r^2 = 0.947$ between SUVA$_{254}$ and Fe in summer samples, $n = 10$). High concentrations of iron (> 2 mg L^{-1}) were shown to form complexes with humic substances and increase DOM absorbance

(Maloney et al., 2005; Xiao et al., 2013). During the autumnal turnover, CDOM-Fe complexes from bottom waters are exposed to photochemical reactions at the surface, potentially generating hydroxyl radicals that dissociate carboxyl groups from humic substances. These reactions can lead to lower molecular weight carbon components at the same time as increasing the water clarity (Brinkmann et al., 2003). The spectral slope values indicate that algal-derived proteins (S_{289}, Galgani et al., 2011) were more abundant in summer surface waters when primary production and Chl *a* were highest, and at the same time fulvic and humic acids (S_{382}) also seemed more abundant than in winter. Algal proteins are generally highly available to heterotrophic organisms and were likely supporting the higher summer BP (Kritzberg et al., 2004). Nevertheless, Xiao et al. (2013) showed how high Fe concentrations, such as found in bottom waters, can significantly lower DOM absorption slopes, thus interpretations of bottom water S_λ should be done cautiously.

4.3 Thaw pond microbial food web

Primary production rates in summer at the surface of thaw ponds were in same range as in other arctic and subarctic lakes (Lizotte, 2008), while in late winter snow and ice cover prevented in situ PP. However, when exposed to light, the production of carbon by the winter phytoplankton community was in the same range as the heterotrophic production, suggesting that the high phytoplankton biomass encountered during late winter were made of mixotrophic species that switched from hetero- to autotrophic production at ice-out. Similarly, the high Chl *a* and PNF biomass in the light-limited bottom waters in summer were most likely composed of mixotrophs. Many species of Chrysophycaea, Cryptophyceae and Dinophyceae are known to be 99 % mixotrophic (Olrik, 1998 and references therein). Chrysophyceae were dominating the phytoplankton community in KWK2 and KWK20 (Dupont, 2008; L. Forsström, unpublished data). Many Chrysophyceae species have flagella, and thus can thrive in sheltered humic ponds that have been shown to favor diurnal migrations of phytoplankton (Jones, 1991). This is especially advantageous in steeply stratified and shallow ponds where phytoplankton can migrate within a few hours (Arvola et al., 1991), and are able to use nutrient-rich hypolimnetic waters (Salonen et al., 1984). The high nutrient concentrations in bottom waters likely explain the high biomass of PNF observed in these waters. Anoxic bottom waters were also devoid of *Daphnia* sp. (M. Wauthy et al., unpublished data) providing to phytoplankton a refuge from grazing. Absence of light, hypoxia and low temperatures further prevent photo-oxidation of algal pigments, preserving them for extended periods (Vallentyne, 1960). Thus some of the Chl *a* and PNF encountered at the bottom may have been from dead yet still not degraded cells. Another factor that could have caused bias in very high bottom water Chl *a* values is the occurrence of chlorophyll *b* containing green-sulphur bacteria that are known to colonize the anoxic layer of the studied ponds (Rossi et al., 2013), and that may interfere with the spectrophotometric analyses of Chl *a*. However, green-sulphur bacteria were not found in all ponds with high values of Chl *a*.

BP and BB were strongly linked to CDOM originating from a terrestrial source (high SUVA_{254} and a_{320}), indicating a positive link between bacterioplankton and terrestrial carbon (Tranvik, 1988; Crump et al., 2003). These results are in accordance with the experiment from Breton et al. (2009) which showed that bacterioplankton in thaw ponds was more carbon than nutrient-limited (glucose was used as a labile carbon source). On the contrary to several previous studies (Granéli et al., 2004; Säwström et al., 2007; Roiha et al., 2012), the amount of DOC did not seem to control the BP in our study. During the long ice-covered winter period, bacterioplankton was likely degrading the particulate carbon accumulated during the previous open water season, and producing dissolved compounds, explaining the DOC maximum in late winter. The studies that reported a positive correlation between DOC and BP have been conducted in summer, when BP and DOC concentrations were highest, but without necessarily taking into account the variability in DOC type, which had a dominant role in our study.

The presence of a mixture of autochthonous and allochthonous carbon may have helped in making the terrestrial carbon available to bacteria. Phytoplankton and macrophytes apparently produced significant amounts of dissolved carbon in surface waters during summer as indicated by the larger S_{289} peak. This carbon is considered more labile (lower molecular weight) and with a higher nutritional value to heterotrophs (Kritzberg et al., 2004; Brett et al., 2009). The availability of high quality phytoplankton carbon during summer possibly enhanced the bacterial use of more recalcitrant terrestrial carbon though the priming effect (Bianchi, 2011), that is a small supplement of nutritionally rich algal cells increasing bacterioplankton terrestrial carbon assimilation.

Correlation between TSS and TP ($r = 0.903$, $p < 0.001$, $n = 15$) indicates that phosphorus was binding to particles, which may be more accessible to attached bacterioplankton than to phytoplankton in summer surface waters where SRP concentrations were low. The high proportion of particle-attached bacterial abundance (62 ± 30 %) and productivity (59 ± 30 %) in thaw ponds suggests that particle attachment is beneficial. Although studies have shown that BP is often nutrient-limited (Kritzberg et al., 2004; Vrede, 2005), there were no correlation between BP and nutrients in thaw ponds.

One possible additional explanation for the difference between winter and summer BP is the difference in temperature that is known to have a large impact on production (Adams et al., 2010). On the other hand, bacterial communities are known to adapt at low temperatures, and some communities can have multiple temperature maxima (Adams et al., 2010). In our study, the highest BP was found in relatively cool bottom waters. Moreover, bacteria biomass (BB) was not correlated to temperature, although several studies found temperature as a main driver of bacterial biomass (Ochs et al., 1995; Rae and Vincent, 1998). Trophic interactions certainly contributed to the observed patterns in microbial abundance. Rotifers are the dominant zooplankton group in the studied thaw ponds, while the cladoceran community is composed of a few *Daphnia* sp. observed only at the surface (Bégin, 2014). These two zooplankton groups were only found in summer, when they could exert a grazing pressure on bacteria and phytoplankton, but experiments would be needed to confirm the extent of grazing. We tentatively estimated the top-down control of nanoflagellates on bacteria, using the average nanoflagellate ingestion rate of $0.66\,\mathrm{pg\,C\,cell^{-1}\,d^{-1}}$ measured for *Dinobryon* sp. in Svalbard (Laybourn-Parry and Marshall, 2003). From these calculations, it seems that nanoflagellate grazing on bacteria could have been efficient enough in late winter when the grazing potential exceeded 100 % of the BP, while summer removal estimations corresponded to only 1.7 % at the surface and 9.3 % at the bottom of the BP, possibly contributing to explaining the accumulation of BB in summer

In winter, the lack of PP and allocthonous sources of carbon, and a DOM pool composed by a large fraction of molecules with low aromaticity (low SUVA_{254} and S_{289}) suggest that intensively recycled DOM formed the basal organic carbon pool in thaw ponds. This carbon was channeled to the top of the food chain by bacterial grazers (nanoflagellates) and to their predators (*Chaoborus* sp.), as suggested by the mixing model results indicating that *Chaoborus* was more dependent on terrestrial carbon in winter. Similar results showing the increasing importance of terrestrial carbon to zooplankton in winter have also been reported in the subarctic lake Saanajärvi in Finland, where *Daphnia umbra* was almost entirely dependent on terrestrial carbon under the ice (Rautio et al., 2011b). During summer, a lower dependence on terrestrial carbon was likely because algal-derived carbon was more available (high S_{289} and PP), when nearly 70 % of *Chaoborus* carbon had an algal origin in the majority of the ponds.

We also considered whether methane-oxidizing bacteria were included in the zooplankton diet as inferred from the mixing model results. These bacteria are known to occur in environments where both oxygen and CH_4 are available (Hanson and Hanson, 1996), and they were suggested to contribute to zooplankton diet (Kankaala et al., 2006). The metalimnion of thaw ponds, where there is more CH_4 and still some O_2, is a potential living habitat for methanotrophs, relatively abundant in the studied ponds (Rossi et al., 2013). However, methanotrophs are known to have highly negative δ^{13}C values (< -60 ‰), while in our study the *Chaoborus* δ^{13}C values always fell between the algal (median -40 ‰) and terrestrial (-27 ‰) end-members. Therefore, although methanotrophs were present, they did not seem to have a significant role in *Chaoborus* diet.

5 Conclusions

Low light intensity, strong stratification and high concentrations of CDOM in subarctic thaw ponds are the main drivers creating an environment highly beneficial to heterotrophs. We have also shown some important differences in their ecosystem dynamics between winter and summer. Although a high biomass of bacterioplankton is found under the ice, the ponds are producing relatively small amounts of carbon in late winter, likely caused by the lack of fresh carbon inputs and its associated priming effect. Nevertheless, the ponds are accumulating GHG during winter. The relatively high phototrophic biomass and primary production potential encountered under the ice are at the same level as the heterotrophic biomass and production, indicating the importance of mixotrophy in winter. In summer, fresh primary production and terrestrial carbon inputs enhance the heterotrophic production. Although a higher phototrophic (mixotrophic) biomass is encountered in summer, primary production is restricted by light and space and is significant only at the pond surface, thus the heterotrophic carbon production remains significantly higher. Consequently, GHG continue to accumulate in hypolimnetic waters during this strongly stratified summer period, and are most likely released during the autumnal turnover period, in addition to the constant emissions of GHG throughout the summer from the highly supersaturated surface waters.

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Table 1. Limnological properties of the subarctic ponds sampled in late winter and during summer at the surface and bottom of the water column, including pH, conductivity (Cond.), total phosphorus (TP), total nitrogen (TN), soluble reactive phosphorus (SRP), total suspended solids (TSS), particulate organic carbon (POC) and iron (Fe).

Site	pH	Cond. (µS cm^{-1})	TP (µg L^{-1})	TN (µg L^{-1})	SRP (µg L^{-1})	TSS (mg L^{-1})	POC (mg L^{-1})	Fe (mg L^{-1})
Winter								
KWK 2	6.6	60	61.9	957.4	20.8	2.7	0.8	n/a
KWK 6	6.8	49	50.6	687.8	7.7	3.7	1.1	n/a
KWK 12	6.6	46	73.2	1038.4	18.4	4.1	1.2	n/a
KWK 20	6.7	52	180.7	1301.6	47.1	53.9	16.6	n/a
KWK 23	6.4	42	119.3	802.7	33.9	23.5	6.8	n/a
Summer surface								
KWK 2	7.4	38	34.9	289.3	1.2	3.4	0.9	0.3
KWK 6	6.9	61	43.9	227.9	0.9	7.2	2.3	0.2
KWK 12	7.3	36	23.9	311.9	0.7	2.6	0.9	0.3
KWK 20	7.5	47	92.6	263.4	7.1	14.2	1.8	0.5
KWK 23	7.1	48	78.0	227.9	5.7	16.1	2.1	0.4
Summer bottom								
KWK 2	6.2	200	341.5	496.1	1.5	27.7	4.4	2.5
KWK 6	6.2	265	197.7	389.4	n/a	13.6	2.3	1.1
KWK 12	6.1	247	207.1	447.6	1.0	37.0	8.8	2.9
KWK 20	6.0	155	377.0	289.3	73.8	85.8	5.7	5.1
KWK 23	6.2	102	431.8	266.7	45.7	126.8	7.8	4.1

n/a = not available

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Carbon dynamics in highly heterotrophic subarctic thaw ponds

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Table 2. Concentrations of carbon dioxide (CO_2), methane (CH_4), and dissolved organic carbon (DOC), and dissolved organic matter (DOM) optical properties, including absorption coefficient of DOM at 320 nm (a_{320}), specific UV-absorbance index ($SUVA_{254}$), and absorption spectral slopes at 289 nm (S_{289}) and 382 nm (S_{382}), of subarctic pond water sampled in late winter and during summer at the surface and bottom of the water column.

Site	CO_2 (µM)	CH_4 (µM)	DOC ($mg\,L^{-1}$)	a_{320} (m^{-1})	$SUVA_{254}$ ($L\,mg\,C^{-1}\,m^{-1}$)	S_{289} (nm^{-1})	S_{382} (nm^{-1})
Winter							
KWK 2	316	14.1	7.7	8.5	0.9	0.0099	0.0155
KWK 6	354	5.1	5.2	3.0	0.5	0.0112	0.0122
KWK 12	215	2.4	10.5	9.5	0.8	0.0105	0.0154
KWK 20	n/a	n/a	10.3	8.1	0.8	0.0125	0.0130
Summer surface							
KWK 23	357	2.5	7.9	6.6	0.8	0.0124	0.0123
KWK 2	72	0.6	5.6	26.4	4.7	0.0141	0.0169
KWK 6	27	0.5	4.1	11.8	3.4	0.0162	0.0135
KWK 12	55	0.3	6.0	26.5	4.5	0.0142	0.0170
KWK 20	71	0.3	7.1	38.9	6.1	0.0145	0.0156
KWK 23	53	0.3	6.3	30.7	5.4	0.0150	0.0161
Summer bottom							
KWK 2	n/a	n/a	6.1	51.5	6.7	0.0109	0.0156
KWK 6	422	145.2	4.2	21.4	4.3	0.0125	0.0173
KWK 12	761	259.0	7.4	67.9	7.4	0.0111	0.0173
KWK 20	815	311.9	9.3	115.6	9.8	0.0107	0.0172
KWK 23	570	131.6	7.5	94.5	10.2	0.0109	0.0171

n/a = not available

Table 3. Phototrophic and heterotrophic properties of subarctic pond water sampled in late winter and during summer at the surface and bottom of the water column, including chlorophyll *a* concentration (Chl *a*), maximum photosynthesis parameter ($P_{\max}$), in situ primary production (PP), pigmented nanoflagellate abundance (PNF), phototrophic picoplankton abundance (PPA), bacterial production (BP), bacterial respiration (BR), bacterial abundance (BA) and heterotrophic nanoflagellate abundance (HNF).

Site	Chl *a* (μg L^{-1})	$P_{\max}$ (mg C m^{-3} d^{-1})	PP (mg C m^{-3} d^{-1})	PNF (×10^{6} L^{-1})	PPA (×10^{5} mL^{-1})	BP (mg C m^{-3} d^{-1})	BR (mg C m^{-3} d^{-1})	BA (×10^{6} mL^{-1})	HNF (×10^{6} L^{-1})
Winter									
KWK 2	2.8	1.2	0	33.0	0.2	0.2	1.3	4.2	2.0
KWK 6	9.9	0.8	0	51.0	0.9	0.5	2.2	11.2	3.3
KWK 12	11.5	5.8	0	29.1	0.7	0.3	1.6	2.5	2.4
KWK 20	2.8	0.8	0	6.3	0.2	0.8	3.0	8.7^{*}	2.4
KWK 23	0.8	1.5	0	10.0	0.1	0.4	2.0	3.7	0.3
Summer surface									
KWK 2	5.4	4.5	2.6	16.3	3.3	27.2	25.7	13.3	0.0
KWK 6	13.4	27.9	15.3	20.0	4.2	37.4	31.2	11.3	0.8
KWK 12	2.2	5.9	3.2	28.8	0.9	31.2	27.9	9.6	0.7
KWK 20	14.3	59.0	26.4	33.1	17.3	15.2	18.0	14.8	1.9
KWK 23	12.3	55.6	15.6	35.0	3.8	45.9	35.3	12.7	0.4
Summer bottom									
KWK 2	180.2	n/a	0.8	149.6	9.4	57.6	40.5	35.7	26.2
KWK 6	87.2	n/a	4.2	201.6	3.0	39.0	32.0	14.3	6.3
KWK 12	158.9	n/a	0.3	72.5	26.8	48.8	36.6	38.0	3.7
KWK 20	203.4	n/a	0.3	n/a	4.0	39.1	32.0	27.2	n/a
KWK 23	37.1	n/a	0.0	4.5	6.2	23.0	23.2	24.3	0.6

[*] BA was calculated from DAPI-stained microscope slide.
n/a = not available

Table 4. Spearman correlations between biological and environmental variables. Only statistically significant correlations are given.

Biological variable	Environmental variable	r	p
Bacteria production (BP)	Temperature	0.600	0.018
	TN	−0.524	0.045
	a_{320}	0.704	0.003
	SUVA_{254}	0.699	0.004
	S_{382}	0.633	0.011
Bacteria biomass (BB)	O_2	0.555	0.049
	Conductivity	0.668	0.007
	TP	0.600	0.018
	TSS	0.521	0.046
	Fe	0.879	0.001
	CH_4	0.588	0.035
	a_{320}	0.825	< 0.001
	SUVA_{254}	0.857	< 0.001
	S_{382}	0.716	0.003
HNF	Conductivity	0.657	0.011
	CH_4	0.636	0.026
Primary production (PP)	Temperature	0.896	< 0.001
	SRP	−0.662	0.007
	TN	−0.827	< 0.001
	DOC	−0.610	0.016
	SUVA_{254}	0.533	0.041
	S_{289}	0.732	0.002
PNF	SRP	−0.732	0.003
	DOC	−0.647	0.012
PPA	TN	−0.665	0.007
	a_{320}	0.825	< 0.001
	SUVA_{254}	0.717	0.003
	S_{382}	0.564	0.029

Table A1. Carbon isotopic signatures (δ^{13}C) of the algae, and the variables that were used to calculate $\delta^{13}C_{algae}$, including the phytoplankton growth rate (μ), the photosynthetic fractionation parameter (ϵ_p) and the isotopic signature of CO_2.

Site	$\delta^{13}C_{algae}$	μ	CO_2 (µM)	ϵ_p	$\delta^{13}CO_{2(aq)}$
KWK 2	−40.3	1.8	71.7	23.1	−17.2
KWK 6	−34.3	1.2	27.3	21.8	−12.5
KWK 12	−41.4	1.5	55.3	23.0	−18.4
KWK 20	−38.7	2.3	71.5	22.6	−16.1
KWK 23	−36.8	2.6	52.8	21.5	−15.3

Table B1. Particle attachment of bacterioplankton in winter, during summer at the surface and bottom of ponds, including sonicated bacterial abundance (BA_T) representing the total abundance, bacterial abundance before sonication (BA_{FL}) representing free-living bacteria, proportion of particle-attached bacteria (BA_P), total bacterial production (BP; as in Table 3), filtered (3 µm) bacterial production (BP_{FL}) and proportion of particle attached bacterial production (BP_P).

Site	BA_T ($\times 10^6\,mL^{-1}$)	BA_{FL} ($\times 10^6\,mL^{-1}$)	BA_P (%)	BP ($mg\,C\,m^{-3}\,d^{-1}$)	BP_{FL} ($mg\,C\,m^{-3}\,d^{-1}$)	BP_P (%)
Winter						
KWK 2	4.2	0.8	81	0.2	0.1	54
KWK 6	11.2	3.2	72	0.5	0.2	54
KWK 12	2.5	0.5	79	0.3	0.2	48
KWK 20	n/a	n/a	n/a	0.8	0.4	47
KWK 23	3.7	1.4	62	0.4	0.4	7
Summer surface						
KWK 2	13.3	5.8	57	27.2	4.7	83
KWK 6	11.3	8.5	24	37.4	3.3	91
KWK 12	9.6	6.0	37	31.2	17.4	56
KWK 20	14.8	4.1	73	15.2	7.0	54
KWK 23	12.7	7.7	40	45.9	18.6	60
Summer bottom						
KWK 2	35.7	11.3	68	57.6	1.7	97
KWK 6	14.3	8.3	42	39.0	1.5	96
KWK 12	38.0	11.2	70	48.8	26.0	47
KWK 20	27.2	3.7	86	39.1	1.0	97
KWK 23	24.3	4.2	83	23.0	26.6	0

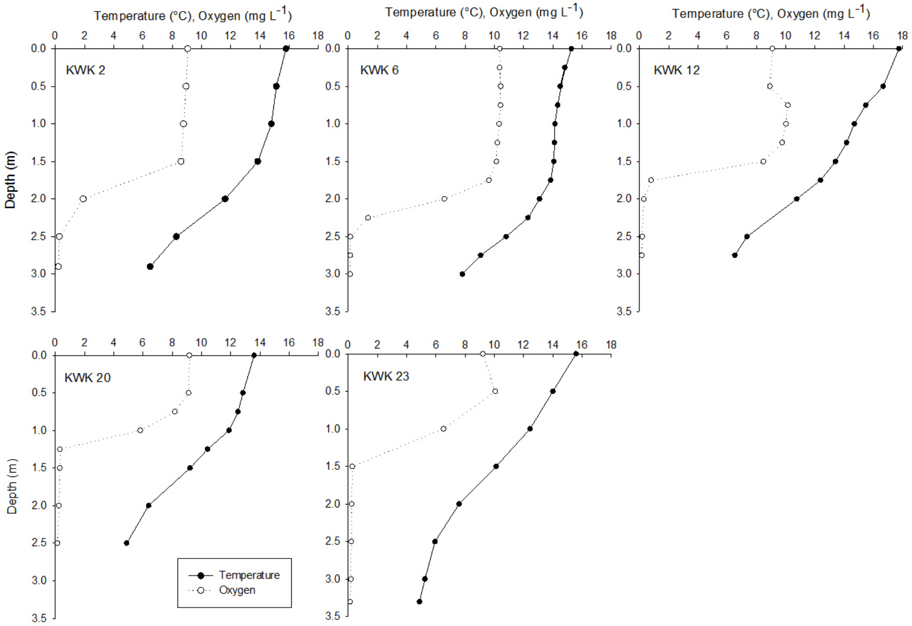

Figure 1. Summer temperature and oxygen profiles from sampled ponds.

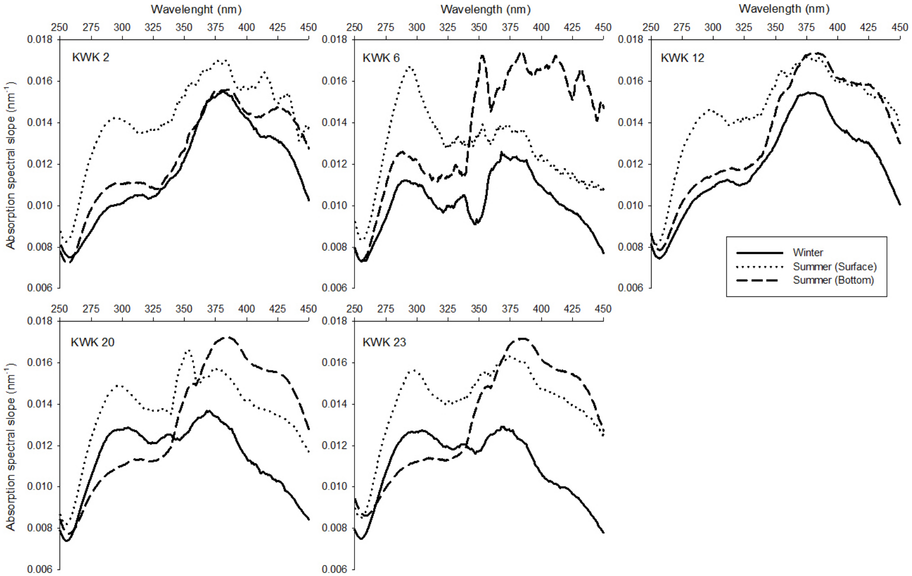

Figure 2. Absorption spectral slope curve (S_λ) of dissolved organic matter as an indicator of the presence of algal-derived carbon (peak at S_{289}) and terrestrial carbon (steady increase in the slopes from 260–390 nm).

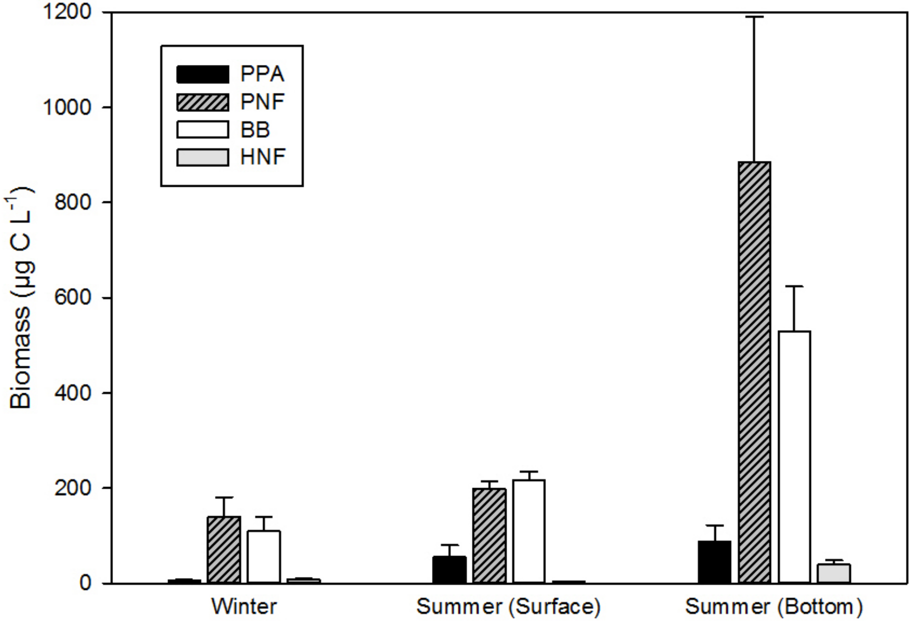

Figure 3. Seasonal changes in the biomass of phototrophic picoplankton (PPA), pigmented nanoflagellates (PNF), bacteria (BB), and heterotrophic nanoflagellates (HNF). Error bars represent standard errors.

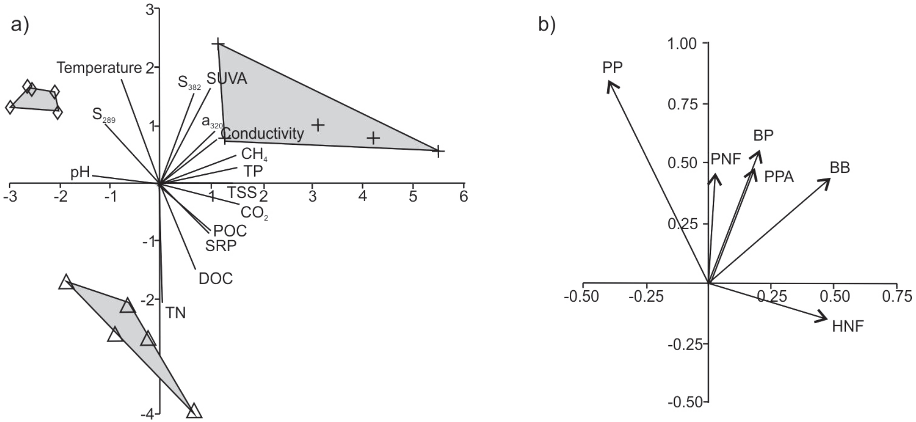

Figure 4. (a) Seasonality of environmental variables illustrated with principal component analysis (PCA) during late winter (triangles), summer surface (diamonds) and summer bottom (crosses). Environmental variables are represented as lines. **(b)** Vectors of biological variables (PP, PNF, BP, PPA, BB, HNF) for the same PCA as in **(a)** (samples not shown). PP = primary production, PNF = pigmented nanoflagellate biomass, BP = bacterial production, PPA = phototrophic picoplankton biomass, BB = bacterial biomass, and HNF = heterotrophic nanoflagellate biomass.

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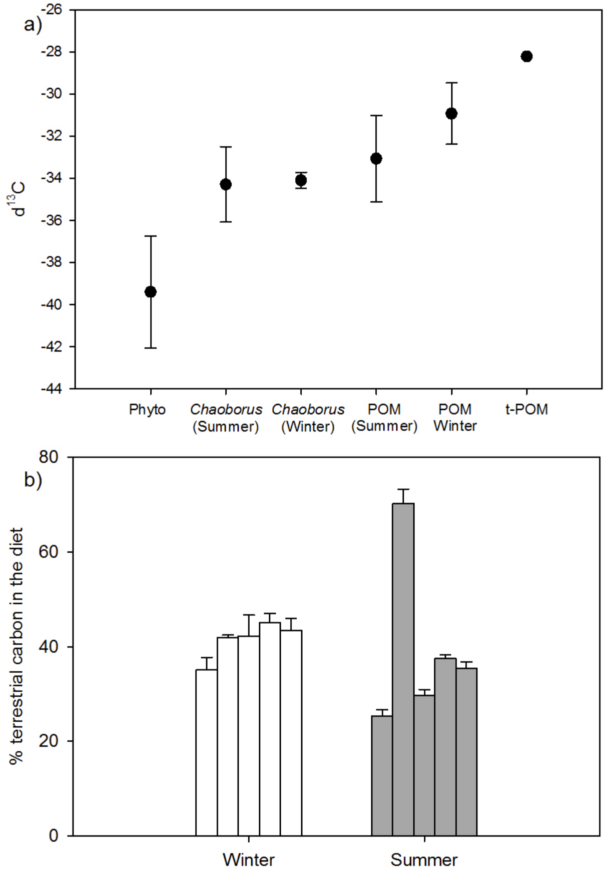

Figure 5. (a) The δ^{13}C isotopic signature of algal carbon (Phyto), *Chaoborus*, particulate organic matter (POM) and allochthonous carbon (t-POM) averaged for samples collected in winter and summer. **(b)** The relative contribution of allochthonous carbon to *Chaoborus* diet in winter and summer for the 5 sampled ponds.