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CARACTÉRISATION LIMNOLOGIQUE ET RÉACTIVITÉ DE LA MATIÈRE ORGANIQUE DISSOUTE DES MARES DE THERMOKARST

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Résumé

Les sols pergélisolés arctique et subarctique contiennent de grandes quantités de matière organique. La fonte accélérée de ces sols aux hautes latitudes nordiques est préoccupante quant au potentiel de transport et de recirculation et de libération de carbone vers l'atmosphère sous forme de gaz à effet de serre qui pourrait s'en suivre. Les mares thermokarstiques formées par l'érosion locale du pergélisol peuvent favoriser la mobilisation de la matière organique dissoute (MOD) et sa dégradation et sont communes dans le paysage nordique. Dans cette étude, nous avons examiné les caractéristiques physicochimiques et biologiques de 57 mares de thermokarst distribuées entre 55 et 73°N. Les mares observées prenaient naissance dans une dépression sur le dessus d'une forme périglaciaire ou à sa périphérie, en présence de pergélisol continu ou discontinu et de différentes densités et dominances de végétation. Nous avons observé que la composition du sol différait d'un site à l'autre, principalement par la présence ou non de tourbe. Les résultats montrent que les mares de thermokarst sont des environnements aquatiques qui présentent une grande diversité, tant dans les propriétés physiques, chimiques que biologiques. Les mares thermokarstiques font contraste avec le reste du paysage aquatique des hautes latitudes majoritairement composé de lacs oligotrophes, alors qu'elles présentent des concentrations en nutriments relativement élevées et un réseau alimentaire microbien actif. Cependant, les concentrations en Chl*a* indiquent une production primaire planctonique réduite dans cet environnement où la lumière est rapidement atténuée. Les résultats montrent que le potentiel de libération de CO_2 et de CH_4 vers l'atmosphère semble lié de façon quantitative et qualitative avec la MOD disponible dans le plan d'eau. La réalisation d'expériences de dégradation microbienne et photochimiques a permis de mieux comprendre les transformations que subit la matière organique une fois mobilisée dans la mare. Les expériences de dégradation de la MOD ainsi que la forte productivité biologique hétérotrophe observée démontrent que le *turnover* du carbone dans les mares est relativement rapide et encore probablement sous-estimé, particulièrement dans les mares avec une forte turbidité inorganique. Le rôle de ces mares dans le cycle du carbone a ainsi été abordé et des suggestions sont présentées pour la tenue de futures études dans l'Est du Canada.

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Avant-propos

Ce mémoire de type « par article » se compose de deux parties. La première partie est constituée d'une brève synthèse en français présentant brièvement la problématique, suivie d'une introduction des connaissances qui développe les thèmes abordés dans la problématique, et finalement la présentation des objectifs de recherche, hypothèses et résultats de mon projet de maîtrise. La deuxième partie se compose de deux chapitres qui sont en fait des articles écrits dans le cadre de la maîtrise. Le chapitre 2 sera soumis à la revue *Global Change Biology* entre le moment du dépôt initial et final avec quelques modifications.

En annexe se trouvent les résultats d'analyses d'échantillons pris dans le cadre de mes deux saisons de terrain. Ces résultats se retrouvent en annexe soit parce qu'il a été jugé trop lourd de les explorer davantage dans le cadre de ce projet de maîtrise ou parce qu'ils avaient été pris dans une perspective exploratoire seulement. Il sera pertinent de consulter ces résultats pour toute personne qui désire connaître plus à fond les mares thermokarstiques. De plus, puisque que plusieurs acronymes sont utilisés dans le texte, un glossaire est disponible ci-après.

Voici une description de la contribution des auteurs des articles au projet de maîtrise :

Julie Breton :
Planification du projet
Réalisation des expériences
Échantillonnage
Rédaction initiale et finale des articles

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Glossaire des abbréviations

a_{320} or a_{CDOM}: absorbance de la matière organique chromophorique à 320 nm.

a_{320}/DOC : absorptivité/absorptivity. Absorbance normalise par la concentration en DOC

BP : bacterial production (by leucine incorporation method)

Chl *a* : Chlorophyll a

DO : dissolved oxygen

DOC : dissolved organic carbon (équivalent français : COD pour carbone organique dissous)

DOC_L : dissolved organic carbon that is labile to microbial degradation

FA : fulvic acid (équivalent français : AF pour acide fulvique)

FS : fluorescence synchrone (équivalent anglais : SF pour synchronous fluorescence).

Gt : Gigaton/ne

HA : humic acid (équivalent français : AH pour acide humique)

HI(1 ou 2) : humification index

LMW : low molecular weight

MMW : medium molecular weight

MO : matière organique (équivalent anglais : OM pour organic matter)

MOD : matière organique dissoute (équivalent anglais : DOM pour dissolved organic matter)

MODC : matière organique dissoute chromophorique (équivalent anglais : CDOM pour chromophoric dissolved organic matter)

MOP : matière organique particulaire (équivalent anglais : POM pour particulatre organic matter)

MW : molecular weight

PT : phosphore total (équivalent anglais : TP pour total phosphorus)

SRP : soluble reactive phosphate

TCA : trichloacetic acid

Tg : Teragrams (est équivalent à Gt pour Gigatonne)

TP : total phosphorus

TN : total nitrogen

TSS : total suspended solids (équivalent français : MES pour matière en suspension)

UV : ultraviolet (radiation)

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Première partie

Synthèse

CHAPITRE 1 : SYNTHÈSE

1. Problématique générale

Le milieu nordique est un milieu encore peu exploré relativement à la grande superficie qu'il représente. Cependant, c'est un milieu qui attire de plus en plus l'attention car les écosystèmes arctiques et boréaux jouent un rôle global crucial sur Terre pour plusieurs raisons : (i) ils occupent une grande proportion de la surface terrestre (22%) ; (ii) leur structure et fonctionnement sont sensibles aux changements subtils dans le climat ; (iii) beaucoup de ces changements fonctionnels ont des effets importants sur l'atmosphère (**Chapin et al. 2000**).

Un quart de la surface terrestre de l'hémisphère nord demeure gelée à l'année (pergélisol) (**Gorham, 1991**). Par conséquent, le milieu nordique est largement influencé par les processus liés à la couche active du pergélisol. Selon les prévisions, de grandes étendues de pergélisol sont menacées de disparaître dans les régions polaires et subpolaires (**Camill 2005**). C'est en fait plus de 90% du pergélisol dans les sols arctiques qui pourraient bien fondre dans le prochain siècle (**Pearce 2006**).

Une mare de thermokarst est formée par l'érosion locale du pergélisol et est un phénomène commun dans le paysage nordique. Lors de la formation d'une mare, une partie de la matière organique (MO) de son bassin de drainage peut être mobilisée dans l'eau sous forme dissoute. L'apparition de ce milieu limnétique peut favoriser la transformation de la MO et son transfert vers l'atmosphère (respiration) et les zones côtières marines (ruissellement). En plus de s'y retrouver en très grande quantité, le carbone organique des sols arctiques est typiquement vieux, avec un âge moyen allant du siècle au millénaire (**Schell, 1983 ; Schirrmeister et al. 2002**). Cependant, il règne une controverse au sein du milieu scientifique quant à la possible exportation de ce vieux carbone vers les milieux aquatiques. Par exemple, **Benner et al. (2004)** ont montré que c'est plutôt du jeune carbone qui est mobilisé dans une grande rivière de Sibérie. D'un autre côté, **Zimov et al. (1997)** ont daté du méthane relargué par des lacs nord-sibériens à un âge moyen de 27 200 ans (Pleistocene). Les processus qui produisent, consomment et transforment ensuite cette MO font partie intégrante du cycle du carbone dans les écosystèmes aquatiques. Parmi ces

processus, la photo-oxydation et le catabolisme bactérien produisent du dioxide de carbone (CO_2) et du méthane (CH_4) à des taux qui dépendent des conditions physicochimiques, de la communauté microbienne et de la nature de la MO. Celle-ci peut également être récalcitrante à ces processus et se retrouver éventuellement dans le réseau de drainage vers l'océan.

Le rejet de carbone à partir des zones à pergélisol est préoccupant puisque qu'une libération massive de gaz à effet de serre agirait comme une rétroaction positive sur le climat. Par exemple, la fonte du pergélisol pourrait « larguer » plus de 400 millions de tonnes de CH_4 stockés dans les sols gelés (**Pearce 2006**). Quoi qu'il en soit, la magnitude et même le sens des mécanismes de rétroaction des régions nordiques face aux changements climatiques induits par une augmentation de CO_2 dans l'atmosphère sont un sujet encore disputé (e.g. **Hamilton et al. 1994** ; **Waelbroeck et al. 1997 ; Zimov et al. 1997** ; **Chapin et al. 2000** ; **Payette et al. 2004 ; Smith et al. 2005**). Par exemple, ce phénomène de libération pourrait être de courte durée et être suivi ou contre balancé par la croissance des plantes (un puits de carbone) et donc sans conséquence majeure sur le climat global de la planète. Pour sa part, l'exportation accrue de matière organique vers le milieu aquatique peut avoir un impact important sur les bilans annuels de température et de lumière, qui façonnent littéralement la productivité microbienne (**Williamson et al. 1999**). De plus, la MO représente une source d'énergie transférée en partie à la chaîne alimentaire via les bactéries, dépendamment de sa labilité.

2. Introduction

2.1 Les hautes latitudes et leur rôle prépondérant dans le cycle du carbone

La synthèse des résultats de plusieurs programmes de recherche en milieu boréal et arctique a mis en évidence le rôle important de ces écosystèmes dans le système climatique (**Chapin et al. 2000**). Les hautes latitudes (53-83°N) présentent les plus grandes amplitudes saisonnières de concentration atmosphérique en CO_2 (**Zimov et al. 1996** et références citées) et sont depuis longtemps reconnues comme des joueurs potentiellement importants dans le cycle global du carbone à cause de leur importante réserve de matière organique. Ces réserves représentent de 20 à 60% de toutes les réserves de carbone du sol. Cette quantité de carbone est 1 à 2 ordres de grandeur plus grande que ce qui est transféré annuellement vers l'atmosphère sous forme de gaz par le brûlage des combustibles

fossiles et la déforestation (**Hobbie et al. 2000** et références citées). Les tourbières boréales et subarctiques ont été un puits de carbone majeur (**Gorham 1991**) de l'Holocène jusqu'au début du petit âge glaciaire lors de l'expansion du pergélisol (**Allard et Séguin 1987**, **Worsley et al. 1995**, **Payette et Rochefort, 2001**) qui emprisonna des quantités incroyables de matière organique dans le sol. Par exemple, selon le modèle utilisé, les tourbières nordiques sont le réservoir de 180 à 455 Pg (Petagram = Gigaton) de carbone (**Sjörs 1980**, **Armentano et Menges 1986**, **Oechel 1989, Gorham 1991**) qui s'est accumulé durant la période post-glaciaire. La toundra contient quant à elle environ 300Gt de carbone, dont 80% se retrouve dans le sol sous forme de matière organique partiellement décomposée (**Oechel et Vourlitis 1994**), ce qui représente 27% du contenu en carbone de l'atmosphère. Une modification des échanges de carbone entre la toundra et l'atmosphère pourrait alors affecter significativement les concentrations de CO_2 atmosphérique (**Waelbroeck et al. 1997**).

Les températures qui règnent dans les régions nordiques permettent au sol de rester gelé en permanence à certains endroits et à différentes profondeurs selon la latitude (pergélisol ; voir la section suivante). Ce sont de très grandes quantités de matière organique stockées depuis des milliers d'années qui seraient rendues disponibles à la dégradation aérobie et anaérobie si le pergélisol fondait.

2.2 Le pergélisol

Au Canada, le pergélisol est ainsi défini : « sol (ou roche) qui se maintient à une température égale ou au dessous de 0°C pendant au moins 2 ans » (**C.A.R.G. 1988**). Le pergélisol recouvre près du quart de l'hémisphère nord (**Gorham 1991 ; Zhang et al. 1999**) ; au Canada, il couvre 40-45% de la surface (**Payette, 2001**) et plus du tiers du territoire québécois.

Traditionnellement, on a subdivisé les régions pergélisolées en deux zones : la zone de pergélisol continu et la zone de pergélisol discontinu (**Figure 1**). Avec l'avancement des recherches et des inventaires, la définition a été raffinée.

L'aspect que prend le pergélisol, sa dureté (cohérence) et le type de glace qu'il contient découlent d'une série de facteurs qui sont principalement : la composition granulométrique, les structures sédimentaires d'origine du dépôt meuble, le régime

thermique et la présence de tourbe en surface ou d'horizons organiques enfouis. Différentes formes de relief sont associées à la composition variable du pergélisol : les pingos, les palses, les buttes cryogéniques (ou lithalses), les polygones à coins de glaces, les sols striés, les buttes gazonnées et les thufurs, les nappes et les lobes de gélifluxion (**Allard et al., rapport préliminaire**). Nous nous attarderons pour le moment sur la description des palses, lithalses et polygones à coin de glace puisque ce sont ces types de relief que nous avons observés lors de la présente étude.

2.2.1 Les palses

Ce sont des buttes de pergélisol qui se forment dans des tourbières de la zone de pergélisol discontinu (**Figure 1 d**). Elles peuvent atteindre 10 m de hauteur mais la moyenne est d'environ 5 m. Les plus petites sont rondes et ne mesurent que quelques mètres de diamètre. Les plus grandes, habituellement de forme allongée, ont des dimensions moyennes maximales de 30 m de largeur sur 100 m de longueur et sont appelées plateaux palsiques. La limite nord de leur aire de distribution correspond approximativement à la limite des arbres (**Allard et al., rapport préliminaire** ; **Allard et Seguin 1987**). La majorité des palses du Québec se répartissent dans des tourbières qui recouvrent des étendues de limons argileux marins (**Allard et al., rapport préliminaire**). Le mode de formation et le cycle de vie des palses sont documentés par **Seppälä (1986)**. La formation d'une palse débute lorsque le couvert de neige est localement assez mince pour permettre au front de gel de pénétrer suffisamment profondément pour prévenir la fonte complète en été. Cela soulève le couvert de tourbe en cet endroit. Les hivers se succédant permettent au front de froid de pénétrer de plus en plus profondément, exacerbant le soulèvement. Alors que la surface se soulève, le vent devient de plus en plus efficace pour assécher la surface tourbeuse et la préserver d'une accumulation importante de neige. Lorsque le gel atteint le sol sous-jacent, le stage de maturité de la palse est atteint. Suite à l'adoucissement du climat ou à une modification du régime des précipitations, les palses peuvent commencer à fondre pour éventuellement faire place à des cavités et à des mares de thermokarst. Les mares se formant en périphérie des palses ont été échantillonnées pour ce projet. Cependant, une palse qui est complètement dégradée peut donner naissance à une mare à l'endroit où était le sommet de la palse jadis.

2.2.2 Les lithalses ou buttes cryogéniques

Ce sont des buttes aux dimensions comparables à celle des palses et qui se développent dans des sols limoneux et argileux (**Figure 1 c**). Grossièrement, les buttes minérales cryogènes sont au milieu minéral ce que sont les palses au milieu tourbeux. Cette constatation d'ordre général ne saurait toutefois traduire toute la complexité des processus morpho-génétiques responsables de leur formation et de leur diversité. Elles sont reliées essentiellement à l'évolution progressive et régressive du pergélisol dans les sédiments minéraux, en l'absence d'une couche de tourbe (**Payette et Séguin 1979** et références citées). La plupart se situent au-delà de la limite des arbres (toundra arbustive) dans la zone de pergélisol discontinu et abondant. La surface de la plupart des buttes est parsemée de terre, appelées ostioles (**Allard et al., rapport préliminaire**). L'analyse sédimentaire d'une lithalse à l'un des sites que nous avons visité a été effectuée par **Calmels et Allard (2004)**. Les résultats montrent que le sol est principalement composé, en ordre décroissant, d'argile, de limon, de matière organique, de carbonates et de sable. Dans la présente étude, les mares échantillonnées en présence de cette forme périglaciaire avaient majoritairement pour lieu de naissance une dépression sur le dessus de la butte, bien que quelques mares de périphérie aient aussi été échantillonnées.

2.2.3 Les polygones à coins de glace

Les côtés des polygones sont découpés par des sillons de quelques décimètres sous lesquels se forment au fil des ans les coins de glace. Les polygones en coins de glace se situent principalement en zone de pergélisol continu. C'est un phénomène naturel (non pas causé par le réchauffement du climat) qui se produit dans la couche active du pergélisol, cette couche superficielle qui gèle et dégèle à chaque année. Ils dessinent des figures géométriques (cellules) imparfaites de quatre à sept côtés dont le diamètre moyen est d'environ 20 m (**Figure 1 e**). Le plus souvent, ces polygones sont dit « à centres déprimés », les sillons encadrés de bourrelets étant plus hauts que le centre des polygones qui demeurent souvent très humides (**Allard et al., rapport préliminaire**). Leur origine a été expliquée par **Lachenbruch (1962)**. Quand le sol gèle en hiver, un réseau polygonal de contrainte se développe, ce qui sépare et crée des craques dans le sol. Au printemps, l'eau de surface s'infiltre dans les craques, gèle et crée des filons de glace de quelques millimètres d'épaisseur. Avec les années, le sol craque à peu près à la même place et des filons de glace successifs se combinent pour faire des coins de glace. Quand ces formations fondent, cela crée des mares sur les polygones affaissés et dans les canaux où

se trouvaient les coins de glace. Dans la présente étude, l'eau a été échantillonnée autant dans les sillons périphériques que dans les mares du centre déprimé des polygones.

2.2.4 La fonte du pergélisol

L'existence et la persistance du pergélisol sous un site donné reposent sur un principe essentiel : il faut que la température moyenne annuelle à la surface du sol soit inférieure à 0°C, dans lequel cas le sol perd plus de chaleur qu'il n'en reçoit de l'atmosphère, ce qui le maintient gelé (**Allard et al., rapport préliminaire**). En réponse à des perturbations, comme un feu ou un réchauffement du climat, le pergélisol peut fondre de façon différentielle, créant des surfaces topographiques irrégulières. La fonte à la surface du sol peut rapidement donner naissance à des mares, accélérant la fonte sous la surface et l'advection de chaleur additionnelle dans la mare par ruissellement. Éventuellement, un talik (une couche de sol non gelé en haut du pergélisol et sous la mare) peut se former. Si la taille du talik est suffisante pour pénétrer le sol sous-jacent ou se connecter à une couche sous-jacente suffisamment perméable, la mare peut alors se drainer (**Yoshikawa et Hinzman 2003**).

2.2.5. Les mares thermokarstiques

Nous appelerons mares de thermokarst (ou mare thermokarstiques), dans le cadre de cette étude, les mares qui se sont formées suite à la fonte du pergélisol en périphérie ou dans une dépression sur le dessus d'une des formes périglaciaires nommées plus haut (son *cycle de vie* est décrit dans l'introduction du chapitre 2). La mare thermokarstique est un petit écosystème aquatique à part entière qui peut demeurer présent à court ou moyen terme, jusqu'au drainage éventuel de son eau (en absence de l'imperméabilisation du sol par les argiles) ou jusqu'à la colonisation par les plantes aquatiques par le phénomène de terrestrialisation (**Payette et al. 2004**). Elles peuvent aussi fusionner entre elles pour former de plus grandes étendues d'eau. La mare thermokarstique est un écosystème aquatique qui fait partie du paysage nordique au Canada, tant au Nunavik (nord du Québec) que dans le territoire du Nunavut, deux endroits visités dans le cadre de notre étude. À titre informatif, elle porte souvent le nom de « thaw lake/pond » dans la littérature.

Puisque très peu d'études se sont attardées à ce type d'écosystème (voir introduction du Chapitre 2 et sections suivantes), leur description est fragmentaire et leur répartition dans l'ensemble du paysage est mal connue. Une brève revue des connaissances actuelles sur les milieux humides des hautes latitudes paraît ici appropriée.

2.3 État des connaissances sur les écosystèmes aquatiques nordiques

2.3.1 Des milieux principalement oligotrophes?

Les écosystèmes aquatiques des hautes latitudes se situent dans un paysage avec faible lessivage chimique et où l'influence anthropique directe est minimale. Cette situation produit typiquement des systèmes d'eau douce ultra-oligotrophes car l'apport de nutriments et de carbone organique des alentours est faible (e.g. **Pienitz et al. 1997a, b**).

Dans une caractérisation extensive sur 24 lacs de hautes latitudes, **Pienitz et al. (1997b)** ont montré que la plupart des lacs sont peu profonds (Z_{max} = 2.5 à 25 m; moyenne = 8,2 m), pauvres en éléments nutritifs (3.4 à 12.7 µg L^{-1} en phosphore totale, moyenne = 6,6 µg L^{-1}) et de faible alcalinité. De manière typique, l'eau était pauvre en solutés (conductivité électrique près de 0 à 100 µS cm^{-1}), et son pH variait de légèrement acide à alcalin (6.2 à 8.9). Les concentrations de tous les éléments nutritifs et ions majeurs ont montré des tendances identiques, c'est-à-dire qu'elles diminuaient avec l'augmentation de la latitude, les concentrations les plus élevées se trouvant généralement dans les lacs méridionaux avec forêts de conifères dans le bassin versant. La concentration en Chl *a*, mesure grandement utilisée comme indicatrice de biomasse phytoplanctonique et de statut trophique (**Vollenweider 1968**), s'étalait de 0.1 to 20.4 µg L^{-1}. Cependant, la plupart des sites d'études étaient de statut oligotrophe. D'un autre côté, des études de fertilisation ont montré que des lacs arctiques peuvent tout de même supporter de forte productivité primaire malgré les faibles températures (**O'Brien et al. 1992; Douglas and Smol 2000**). Aussi, **Kling et al. (1991)** ont démontré que les lacs et rivières arctiques du nord de l'Alaska relarguaient du CO_2 dans la majorité des 29 écosystèmes aquatiques à l'étude, une indication que ces systèmes sont essentiellement hétérotrophes (**Raymond et al. 2000; Hanson et al. 2003; Urabe et al. 2005**). Cette tendance des milieux aquatiques à être sursaturés en CO_2 et à représenter une source de carbone pour l'atmosphère est bien connue dans les milieux tempérés (**Cole et al. 1994; del Giorgio et al. 1999**).

2.3.2. Les mares et le pergélisol dans les régions nordiques

Les mares sont abondantes dans la toundra (**e.g. Hobbie 1980; Sheath 1986; Douglas et Smol 2000).** Les mares claires et peu profondes sont une composante très importante du paysage de haute latitude et une classe importante d'écosystème d'eau douce. On commence tout juste à mieux connaître ces mares. Par exemple, du point de vue biologique, on sait que la biomasse phytoplanctonique et la productivité sont faibles dans ces eaux à cause des limitations en nutriments (**Alexander et al. 1980**) et du broutage par le zooplancton, qui forme souvent le sommet de la chaîne alimentaire dans cet écosystème (**Hansson et al. 1993**; **Rautio 2001**). Cette inconsistance entre une faible productivité primaire et une forte concentration en zooplancton dans cet écosystème s'explique par l'accès du zooplancton à des ressources additionnelles de nourriture. **Rautio et Vincent (2006)** ont montré en effet que les tapis microbiens joue un rôle important dans le soutien de la biomasse zooplanctonique. Les tapis microbiens sont des structures étagées de groupes de microorganismes physiologiquements différents, présents dans une variété d'environnement où le broutage est limité. La strate du dessus est typiquement dominée par des phototrophes, comme des cyanobactéries, des diatomées et des bactéries vertes non sulfureuses (**Rooselers et al. 2007** et références citées). La faune de macroinvertébrés a déjà été étudiée dans 68 mares en Alaska (**Maciolek 1989**). La richesse des mares étaient élevée avec l'occurrence des taxons suivants : Trichoptère, Hémiptère, Diptère, Pelecypoda, Isopoda, Coleoptera, Gastropoda and Oligocheta dans 50% des mares. Également, **Vézina et Vincent (1997)**, ont caractérisé les communautés cyanobactériennes de mares nordiques et leur environnement, incluant des mares thermokarstiques sur l'île Bylot, un de nos propres sites d'études. Ils ont montré que les cyanobactéries y sont des constituants majeurs de la communauté microbienne, *Synchococcus spp.* et les Oscillatoriaceae y étant nettement dominants. Des études se sont également intéressées à l'effet de la dégradation du pergélisol sur la végétation (e.g. **Jorgenson et al. 2001**; **Lloyd et al. 2003).** Par exemple, il semble que les arbustes et arbres soient restreints au bourrelet périphérique dans les zones grandement affectées par le pergélisol, en grande partie pour des questions de drainage.

Il n'existe pas à notre connaissance d'étude écologique s'attardant spécifiquement à la description des mares de thermokarst. En effet, il n'est souvent pas spécifié si les mares en question sont le résultat d'une simple dépression dans le sol où l'eau s'est accumulée (rock ponds), ou le fruit d'un processus thermique comme c'est le cas avec la mare de

thermokarst. De plus, une étude préliminaire nous a démontré que les mares de thermokarst sont plus souvent qu'autrement des environnements très productifs et rarement oligotrophes, contrairement aux mares rocheuses et aux lacs très répandues dans le paysage nordique, comme l'indique les études citées plus haut. **Jonsson et al. (2003)** ont démontré que des lacs du nord de la Suède étaient également des sources de CO_2 pour l'atmosphère, et que la pression partielle en CO_2 était corrélée à la concentration en carbone organique dissous. Une autre étude des flux de CO_2 et de CH_4 sur des mares des Basses-Terres de la Baie d'Hudson de **Hamilton et al. (1994)** est d'un intérêt particulier pour nous. Ils ont mesuré le flux de ces deux gaz dans les mares mais aussi celui des surfaces végétales environnantes et ont constaté de grandes différences entre les deux surfaces : les flux enregistrés pour les mares étaient de 3-30 fois plus élevés que pour les milieux environnants colonisés par de la végétation dans le cas du méthane, et de magnitude mais de sens inverse (flux vers l'atmosphère) pour le dioxyde de carbone. Ainsi donc, un changement dans le ratio surface végétale versus surface occupée par des mares aurait un grand impact sur les flux de ces gaz dans cet environnement. Si de plus en plus de mares de thermokarst se formaient par la suite des changements climatiques et que l'écosystème réagissait de la même façon que dans l'étude de **Hamilton et al. (1994)**, les flux risqueraient d'augmenter notablement de façon locale. Il resterait à savoir si cette augmentation serait perceptible à une échelle plus globale. D'un autre côté, dans la même région, **Macrae et al. (2004)** ont mesuré que dans certaines mares au contenu hautement organique, le flux de carbone est plutôt inverse (puits de carbone). Cependant, les mares au fort contenu en sédiments minéraux présentaient un flux positif vers l'atmosphère. Dans cette étude, on conclut que le rôle de puits ou de source de carbone des mares n'est pas encore bien arrêté et tend à dépendre du futur régime des précipitations, qui risque d'être bouleversé dans le cadre des changements climatiques (en hiver comme en été). Selon ces auteurs, il est encore trop tôt pour statuer sur le rôle des mares dans le cycle global du carbone. Toutefois, le rôle potentiel de ces écosystèmes à titre de source dépendrait selon eux largement de l'habileté du milieu à « mobiliser » le carbone du milieu environnant. Finalement, des mesures du contenu en méthane dans le pergélisol ont été effectuées par **Brouchkov et Fukuda (2002)**. Leurs résultats montrent que les concentrations de méthane et de dioxyde de carbone étaient corrélées avec le contenu en eau dans le sol gelé. De plus, le pergélisol plus « vieux » contenait des concentrations en méthane plus élevées que le pergélisol plus moderne.

Les études qui traitent plus spécifiquement des mares ou lacs de thermokarst, ces milieux aquatiques qui naissent de la fonte du pergélisol, sont plus rares, et concerne majoritairement les lointaines contrées Sibériennes (e.g. **Zimov et al. 2001** (flux de méthane); **Walter et al. 2006** (flux de méthane); **Smith et al. 2005** (distribution)), ou de l'Alaska et de l'Ouest du Canada (**Billings and Peterson 1980; MacKay 1990; Hinkel et al. 2003**). Il est important de noter ici que les deux continents présentent de nombreuses différences. Par exemple, la composition du sol où prenne naissance les mares n'est pas la même (plus de carbone dans le sol sibérien) et l'aire recouverte de lacs de thermokarst est plus grande en Sibérie. Il y a cependant quelques études qui se sont déroulées dans l'Est du Canada, mais elles s'attaquent davantage aux changements dans la distribution et aux étapes de développement des mares et du pergélisol (e.g. **Laprise et Payette 1988; Laberge et Payette 1995**) que du milieu limnétique en tant que tel. Ces études montrent d'ailleurs que le pergélisol est surtout en dégradation dans les aires étudiées. En fait, la plupart des études sur les processus thermokarstiques traitent surtout d'aspects d'ordre géologique et géomorphologique (e.g. **Allard et Séguin 1987; Harris 2002**; **Luoto et Seppälä 2003**), ou focalisent davantage sur les régimes hydrologiques qui y sont associés (e.g. **Schwamborn et al. 2002; Yoshikawa et Hinzman 2003**). Les causes et les conséquences du développement thermokarstique dans les zones de pergélisol sont abondamment documentées (e.g. **French 1987**; **Fortier et Allard 2004**). Des perturbations de toute sorte (e.g. feu, changements climatiques) sont à l'origine des thermokarsts. Quelle qu'elle soit, la perturbation a comme conséquence d'augmenter la température et d'initier la fonte.

Il est donc clairement nécessaire d'étudier les mares thermokarstiques, particulièrement dans l'Est du Canada, et notamment les aspects limnologiques impliqués. Une description de l'environnement et de la réactivité de la matière organique présente est un premier pas vers la compréhension du rôle potentiel de cet écosystème face aux changements qui bouleversent présentement les hautes latitudes. Avant d'aller plus loin, une introduction s'impose sur la matière organique lorsqu'elle se retrouve sous forme dissoute dans le milieu aquatique.

2.4 La matière organique (MO)

2.4.1. Définitions

Tout d'abord, une définition physique qui différencie MO dissoute (MOD) de MO particulaire (MOP) est nécessaire. La MOD est la portion du matériel organique qui passe au travers d'un filtre dont la taille moyenne des pores est de moins de 0.7 μm (intervalle utilisée de 0.22-1.22 μm). La démarcation est purement opérationnelle et déterminée par l'investigateur. La MO qui entre dans les lacs et les rivières est principalement sous forme dissoute (**Wetzel 2001**). Plusieurs études ont démontré qu'une proportion significative des bactéries peut passer à travers des filtres de porosité 0.7 μm en fibre de verre (**Gasol & Moran 1999**), habituellement utilisés dans le passé. Il est donc préférable et de plus en plus courant d'employer des filtres de 0.2 μm. Attardons-nous particulièrement sur la partie dissoute de la MO car c'est celle-ci que nous avons étudiée dans le cadre du présent document. Il existe plusieurs façons de classifier la MOD dans l'environnement aquatique: taille des molécules, provenance, composition chimique, réactivité, etc. Nous passerons ici en revue la plupart de ces classifications afin de familiariser le lecteur avec cette composante très importante de l'écosystème aquatique.

La matière organique dissoute (MOD) consiste en un mélange complexe de composés provenant de différentes sources continuellement transformé par différents processus. Globalement, elle est composée de substances humiques (acides humiques et fulviques), d'hydrates de carbone, d'acides carboxyliques et d'acides aminés libres et/ou sous forme de protéines. La MOD est une source de carbone organique, d'azote, de phosphore et de soufre pour l'écosystème aquatique (**Aitkenhead-Peterson et al. 2003**). Elle peut être soit de provenance autochtone (synthétisée à l'intérieur même du lac), soit de provenance allochtone d'origine terrestre importée vers le cours d'eau par les airs et surtout l'eau de ruissellement (**Wetzel 2001**). Les sources de MOD autochtone peuvent être diverses mais sont essentiellement dérivées des algues/phytoplancton (e.g. **Baines et Pace, 1991 ; Munster, 1993**) et des macrophytes (e.g. **Wetzel et Manny 1972, Wetzel et Pennhale 1979**). Quand à la MOD d'origine allochtone, les apports sont surtout dominés par le transport advectif des eaux de surface ou souterraines (**Aitkenhead-Peterson et al. 2003**).

Longtemps considéré comme un ensemble de molécules plutôt inertes et homogènes dans le temps et l'espace, la composition de la MOD est encore aujourd'hui relativement peu connue. Cependant, de plus en plus d'outils (voir les sections Méthodes du présent

document) ont été développés afin de mieux la caractériser. Longtemps considérée à tort comme inerte, la MOD est probablement « la composante la plus interactive » des écosystèmes aquatiques (**Findlay & Sinsabaugh 2003**). De plus, elle présente une grande hétérogénéité. Par exemple, les molécules composant la MOD peuvent être regroupées en grandes classes, qui sont en fait un mélange hétérogène de composés ayant des propriétés chimiques similaires (groupement acide, caractère hydrophobe et poids moléculaires) (**McKnight et al. 2003**). Les classements sont divers, mais nous retiendrons trois grands groupes tels que discernés par les 3 principaux fluorophores observés en fluorescence synchrone: les acides humiques, les acides fulviques (tous deux des substances humiques) et les composés protéiques ou composés similaires.

Pour des eaux douces naturelles typiques, la fraction dominante est représentée par les acides fulviques, définies comme les substances jaunes (« *yellow substance* »), représentés par la partie des substances humiques solubles à tous les pH et de poids moléculaire moyen (**Aiken 1985**). Les acides humiques font également partie des substances humiques, mais sont présents en moindre quantité. Le pourcentage de l'ensemble total de la MOD représentée par les acides fulviques est typiquement de 45 à 90%, selon le milieu aquatique dont il est question.

Également, parmi les substances citées plus haut, une partie de la MOD est qualifiée « chromophorique » (MODC) et possède ainsi la capacité d'absorber la lumière, surtout dans la région des UV (voir la section méthode pour plus d'information). Selon sa composition, la MOD peut être réactive ou récalcitrante face aux différents processus de transformations actifs dans le milieu aquatique (**Ogura 1975**).

2.4.2. Les transformations de la matière organique dissoute.

Un des rôles fondamentaux que la MOD joue dans l'environnement aquatique est de servir de source de carbone et d'énergie pour le réseau alimentaire microbien. Les transformations biochimiques de la MOD par les bactéries sont fondamentales pour le maintien de la structure et de la dynamique du recyclage des nutriments et des flux d'énergie à l'intérieur d'un écosystème aquatique (**Wetzel 2001**). Elles représentent en effet le lien entre la chaîne alimentaire « classique » et la communauté d'organismes microscopiques (ce qu'on appelle la réseau alimentaire microbien) qui compose le milieu.

Donc, les processus qui produisent, consomment et transforment la MOD sont importants dans les cycles globaux de carbone, d'énergie et de nutriments (**McKnight et al. 2003**).

Il y a quatre grandes voies menant qui permette à la MOD d'être assimilée par le réseau alimentaire microbien : 1-la prise directe, 2- la prise facilitée par photolyse, 3-la prise facilitée par les ectoenzymes ou 4-la sorption. Chacun de ces processus est régulés par une combinaison de facteurs intrinsèques et extrinsèques. Les facteurs intrinsèques sont les éléments de la voie elle-même et incluent les caractéristiques de la MOD, la cinétique des enzymes et la diversité microbienne. Par exemple, les différents composants qui permettent la prise de MOD par la communauté microbienne résidente va affecter quel monomère sera assimilé. Inversement, la composition du réservoir de MOD va probablement affecter quel consortium de bactéries sera présent et actif à un temps donné (**Findlay et Sinsabaugh 2003**).

De grands progrès ont été accomplis au cours des dernières décennies dans la compréhension des voies par laquelle la MOD entre dans le réseau alimentaire microbien. Une des découvertes les plus importantes a été la reconnaissance que les macromolécules présentes dans le réservoir de MOD peuvent être photo-oxydées en composés plus labiles et ainsi directement assimilées par le bactérioplancton (**Moran and Covert 2003**). En effet, l'absorption de lumière du soleil par la matière organique résulte dans la réduction du poids moléculaire moyen (**Opsahl et Benner 1998** ; **Zepp et al. 1998**), la modification des propriétés d'absorbance de la lumière (**Vodacek et al. 1997** ; **Moran et al. 2000**) et la formation d'une variété de photoproduits (**Bertilsson et Tranvik 1998** ; **Moran et Zepp 2000**). Les photoproduits sont des composés inorganiques (e.g. monoxyde (CO) et dioxyde de carbone (CO_2)) et des molécules organiques qui demeurent partie intégrante du réservoir de MOD et qui généralement ont une plus grande susceptibilité à la dégradation biologique (**Moran and Covert 2003** et références citées).

En résumé, la décomposition de la partie dissoute de la MO résulte en des produits finaux gazeux ou de poids moléculaires inférieurs, et la décomposition de la partie particulaire résulte en des conversions enzymatiques vers des composés solubles qui pourront éventuellement être transformés en gaz ou composés de poids moléculaires inférieurs par les mêmes processus. D'autres informations spécifiques sont données dans les Chapitre 2 et 3.

2.5. Les changements climatiques ou pourquoi s'intéresser aux mares thermokarstiques ?

Nous avons vu plus tôt que les connaissances sur le cycle du carbone en milieu nordique sont fragmentaires, se contredisent parfois et que le rôle de ces milieux en tant que futur puits ou source de carbone est controversé. Or, un changement des flux de carbone dans ces régions pourrait avoir des conséquences énormes puisque les réserves de carbone du milieu nordique sont très grandes. De plus, un changement dans les flux vers l'atmosphère de gaz carbonique ou de méthane pourrait exacerber le réchauffement du climat (flux positif) ou au contraire compenser partiellement le réchauffement (flux négatif), puisque ces deux derniers sont des gaz à effet de serre. Plus particulièrement, le CH_4, qui a un temps de résidence de 9-15 ans dans l'atmosphère, est un gaz à effet de serre au moins 20 fois plus effectif que le dioxyde de carbone sur une période de 100 ans pour la rétention de la chaleur (**EPA 2007**). Le méthane, en plus d'être libéré sous forme dissoute dans l'eau comme le CO_2, peut être libéré par « bullage » (*bubbling*). Ce dernier mode de libération est probablement le plus courant (**Walter et al. 2006;** des informations supplémentaires sont données dans les Chapitres 2 et 3).

Ajoutons à cela qu'il est généralement admis que les latitudes nordiques sont particulièrement sensibles aux moindres changements dans l'environnement **(Vincent et al. 1998)**. À titre d'exemple de cette sensibilité, dans les régions près de la ligne nordique des arbres, les lacs ayant un DOC près de 4 mg L^{-1} sont particulièrement sensibles aux faibles changements de DOC (**Laurion et al. 1997**). Ces résultats montrent que la composition spectrale des radiation UV sous la surface dans les lacs de hautes latitudes, ainsi que l'équilibre UV/visible dans beaucoup de ces écosystèmes est sensible à des changements mineurs dans le contenu en MODC.

Les changements climatiques et leurs impacts sur le milieu aquatique sont encore bien peu connus. Un nombre croissant d'observations dépeint un monde toujours plus chaud et d'autres modifications du système climatique (**IPCC 2007**). La magnitude et même le sens des rétroactions des régions nordiques face aux changements climatiques induits par l'augmentation des gaz à effet de serre dans l'atmosphère sont disputés depuis quelque temps déjà (e.g. **Lashof 1989, Shaver et al. 1992, Oechel et al. 1993, Goulden et al.**

1998). Par exemple, la contribution nette des écosystèmes de hautes latitudes au flux net de CO_2 vers l'atmosphère a été estimé à tour de rôle comme une source de 0.2 Pg C à un puits de 1 Pg C. Ces chiffres sont substantiels comparés à la quantité moyenne de CO_2 dans l'atmosphère (3.5 Pg; **Chapin et al. 2000**). Comprendre les facteurs qui contrôlent les flux de carbone dans les hautes latitudes est essentiel pour pouvoir prédire comment les flux de carbone dans ces régions vont répondre aux changements climatiques qui les affectent actuellement. **Hobbie et al. (2000)** ont d'ailleurs montré toute la complexité des facteurs de contrôle du stockage et du renouvellement du carbone dans les sols de hautes latitudes. Dans cette revue exhaustive des facteurs de contrôle sur le cycle du carbone, nous apprenons que différents calculs des flux de carbone, estimés à partir de différents modèles, ne concordent pas au point de vue quantitatif. Également, l'accent a été mis sur les facteurs de contrôle qui sont uniques aux hautes latitudes et ils ont démontré que les modèles biogéochimiques actuels ne sont pas assez représentatifs des conditions qui y règnent.

Certains auteurs suggèrent un changement de contribution entre le court et le long terme. En observant les changements dans la distribution du pergélisol sur plus de 45 ans, **Payette et al. (2004)** ont suggéré que la terrestrialisation rapide pourrait exacerber les conditions de stockage du carbone et tendre à équilibrer le budget de carbone à l'échelle locale dans la région de la Baie d'Hudson (Est du Canada). Également, un modèle d'échange de CO_2, couplé à un modèle du régime thermique et hydrologique du sol, a montré que la fonte partielle du pergélisol et une augmentation subséquente de disponibilité en nutriments pourraient donner lieu à une augmentation temporaire des émissions de CO_2, suivi d'un emmagasinement suite à une recolonisation par la végétation (**Waelbroeck et al. 1997**).

Qu'il s'agisse de modèle ou d'étude de terrain, les différentes contradictions qui règnent suggèrent que la question est complexe. Puisque les mares thermokarstiques sont formées par la fonte du pergélisol, nous serions en lieu de nous attendre à ce que leurs formations soient un phénomène de plus en plus courant. C'est en effet ce qui a été observé par **Payette et al. (2004)** dans une tourbière subarctique de l'est du Canada où la surface occupée par les étangs a augmenté alors que celle occupée par le pergélisol diminuait. **Smith et al. (2005)** ont confirmé cette tendance à la fonte en Sibérie. Cependant, la surface occupée par les lacs a plutôt diminuée car lorsque la fonte entraîne la rupture du pergélisol sous-jacent, le lac finit par se drainer. Les mares thermokarstiques sont donc des

écosystèmes amenés à apparaître ou disparaître, dépendant de différents facteurs, incluant la perméabilité du sol lorsque le pergélisol a disparu. Chose certaine, elles sont certainement très sensibles aux changements qui s'opèrent présentement dans le climat.

Les processus de transformations de la MOD dans l'eau des mares ainsi qu'un portrait limnologique le plus complet possible sont des informations cruciales pour mieux comprendre la réponse de cet environnement singulier aux changements climatiques. Rappelons-le, la plupart des études les plus complètes sur ce type d'environnement ont eu lieu en Sibérie ou dans l'ouest de l'Amérique du Nord (voir plus haut). Malheureusement, ces données sont pratiquement absentes de la littérature en Amérique du Nord à notre connaissance.

3. Objectifs et hypothèses

3.1. Objectifs

L'objectif fondateur de cette étude est d'examiner le rôle des mares thermokarstiques dans l'exportation de carbone vers l'atmosphère (CO_2, CH_4) et vers les autres milieux aquatiques, éventuellement l'océan. Cet environnement étant fort peu connu, la caractérisation limnologique de cet écosystème dynamique était nécessaire, constituant un premier sous-objectif. Ensuite, comme deuxième sous-objectif, une analyse plus approfondie des mécanismes de dégradation de la MOD était également nécessaire afin de mieux comprendre la dynamique du carbone mobilisée dans l'eau de ces mares. Chacun des deux sous-objectifs fait l'objet d'un chapitre sous forme d'article scientifique en anglais. Une intégration des résultats sera présentée dans la présente synthèse ainsi que dans les discussions des deux chapitres afin d'apporter des éléments de réponse à l'objectif principal du projet.

3.2. Hypothèses

- Les mares thermokarstiques présentent une grande variabilité de caractéristiques limnologiques, tant du point de vue optique, chimique que biologique.
- Cette variabilité se reflètera dans la dynamique (cinétique) de transformation biologique et photochimique de la matière organique dissoute.
- Les mares thermokarstiques sont des milieux à forte productivité biologique microbienne.

- Cette forte productivité se reflètera dans la concentration en gaz dissous (sursaturé par rapport à l'atmosphère).

4. Méthodes

Plusieurs sites ont été visités en 2004 et 2005. Certains sont situés dans le Québec nordique (Nunavik) et un autre au Nunavut. Les sites du Nunavik sont situés près des villages de Whapmagoostui-Kuujjuarapik (55.2°N, 77.3°O) et de Umiujaq (56.6°N, 76.1° O) ainsi que dans la région de la rivière Boniface (57 3° N, 76.1° O). Le site du Nunavut est situé sur l'Île Bylot (73.1°N, 80.0°N). Un total de 58 mares ont été échantillonnées pour la caractérisation et les expériences de dégradation de la MOD ont été effectuées sur 5 de ces mares. Le suivi des propriétés de la MOD fait l'objet d'une section supplémentaire ci-dessous étant donné son rôle central dans l'étude.

4.1 Caractérisation limnologique (voir sections Matériels et Méthodes des articles pour les détails techniques)

La caractérisation limnologique comprenait les mesures suivantes:

- Profils physicochimiques (température, O_2 dissous, conductivité, pH) (certaines mares seulement).
- Séquence temporelle de la température d'une mare sur un an en surface et au fond à l'aide de thermistors.
    - Mesures ponctuelles dans l'eau de surface et du fond des mares (nutriments, anions et cations, MES (matière en suspension), COD (carbone organique dissous), a_{320} (absorption du carbone organique dissous chromophorique), F_{COD} (fluorescence du carbone organique dissous), concentration en pigments et en bactéries)
    - Mesures ponctuelles dans l'eau de fond des mares (nutriments, anions et cations, MES, COD, a_{CDOC}, F_{COD}, concentration en pigments et en bactéries) (certaines mares seulement)
- Mesures ponctuelles et cycles diurnes des concentrations de gaz dissous (certaines mares seulement)

4.2. Transformation de la matière organique dissoute

Cinq mares ayant des propriétés optiques différentes ont été choisies afin d'observer la dynamique des transformations photochimiques et microbiennes de la MOD avec le plus de représentativité possible. Dans les deux cas, l'eau a été pré-filtrée sur 0.2 µm (filtres de

cellulose acetate) afin d'enlever les particules et les bactéries avant de début des expériences. Dans le cas de l'expérience de dégradation photochimique, l'eau a été exposée à la lumière naturelle in situ pour quelques jours dans des bouteilles en téflon (transparentes au UV) et a été sous-échantillonnée de 3 à 4 fois durant l'expérience (durée totale de 78 à 326 heures d'exposition) afin de suivre les changements des propriétés optiques de la MOD. Pour ce qui est de l'expérience de dégradation microbienne, l'eau pré-filtrée a été inoculée en laboratoire avec un inoculum naturel de bactéries (filtrat de l'eau des mares sur polycarbonate 0.8 μm), et les propriétés optiques de la MOD ainsi que les bactéries ont été suivies sur 140 jours sous conditions contrôlées (au noir, dans une chambre environnementale à 20°C) avec un sous-échantillonnage durant l'expérience (à 0, 3, 12, 24, 45, 91 et 140 jours en 2004; à 0, 10, 19, 39, 80 et 140 jours en 2005).

Pour les deux types d'expériences, les changements dans le contenu en carbone organique dissous, les propriétés d'absorption et de fluorescence de la MOD et le compte de l'abondance totale des bactéries ont été suivis.

4.3. Le suivi des propriétés de la MOD

Nous avons défini plus tôt la MOD et discuté de sa composition dans les eaux douces naturelles. Plusieurs outils sont disponibles pour connaître plus spécifiquement sa composition dans un milieu donné. Voici un bref aperçu des propriétés de la MOD et des techniques qui y sont associés, utilisées dans le cadre de mon étude des mares thermokarstiques.

4.3.1 COD et MODC

La mesure la plus commune de la MOD est la mesure du carbone organique dissous (COD). Elle donne une approximation de concentration de matière organique totale dissoute dans l'eau. La technique utilisée est décrite dans le Chapitre 2. La partie chromophorique de la MOD (la partie colorée: MODC), grâce à ses propriétés d'absorption de certaines longueurs d'ondes du spectre, peut être utilisée comme traceur de la dynamique et des caractéristiques de l'ensemble de la MOD. L'absorption par le MODC est souvent responsable de l'atténuation de la plupart des UV (280-400 nm) dans les lacs, rivières et les environnements côtiers (**Morris et al. 1995**, **Laurion et al. 1997**, **Gibson et al. 2000**). Ces propriétés d'absorption ont été analysées dans le cadre de la présente étude par spectrophotométrie.

4.3.2 Fluorescence : généralités

La MODC fluoresce également quand elle est excitée par la lumière dans la région bleue et UV. Le processus de fluorescence est bien expliqué dans **Stedmon et al. (2003).** Bien que l'effet des unités structurales de la MOD sur l'intensité et la longueur d'onde de fluorescence moléculaire est extrêmement complexe et partiellement inconnu, des principes fondamentaux suivants peuvent être avancés: l'intensité va décroître avec une augmentation de la longueurs d'onde d'excitation, la présence de plusieurs accepteurs d'électrons va augmenter et la présence de donneurs d'électrons va diminuer l'intensité de fluorescence, et les molécules plus complexes fluorescent à des longueurs d'ondes plus élevées (**Stewart and Wetzel 1980, 1981, Senesi et al. 1991**). Plusieurs analyses de composés modèles ou d'échantillons d'eau et d'acides fulviques isolés d'une grande variété d'environnement indiquent que les fluorophores avec un anneau aromatique qui présente des liens aliphatique, alcool ou ester montrent habituellement un fort pic de fluorescence à 293-308 nm (correspondant au pic I dans **Lu and Jaffe 2001** et au pic hA dans **Ferrari and Mingazzini 1995),** tandis que d'autres substitutions et systèmes de noyaux aromatiques déplacent le pic de fluorescence vers des longueurs d'ondes plus élevées (**Ferrari and Mingazzini 1995** et références citées; **Lu and Jaffe 2001**; **Belzile et al. 2002).** L'analyse des spectres d'émission et de fluorescence synchrone a été réalisée dans le cadre de la présente étude.

4.3.2.1 Émission

La plupart des connaissances sur les propriétés de fluorescence des substances humiques ont été obtenues à partir de données de spectre simple (**Sierra et al. 2005).** Le spectre d'émission présente un seul pic large dont le maximum d'émission se déplace selon la longueur d'onde d'excitation adoptée (**Sierra et al. 2000). McKnight et al. (2001)** ont développé un indice de fluorescence basé sur un spectre d'émission pouvant facilement être mesuré dans un échantillon d'eau filtré et permettant d'estimer la provenance et les propriétés chimiques des acides fulviques dissous. Ils ont constaté que le pic d'intensité de fluorescence se trouve à des longueurs d'ondes plus courtes dans les échantillons où la MOD était principalement dérivée de microbes que pour les échantillons dont la MOD provenait des plantes et du sol. Le ratio de l'intensité de fluorescence à 450 nm sur celui à 500 nm d'un spectre d'émission, pour une excitation à 370 nm, sert d'indice (appelé

fluorescence index ou FI) de la provenance de la MOD (Voir Chapitre 2 pour plus d'information).

4.3.2.2 Fluorescence synchrone

La Fluorescence synchrone (FS) tire plutôt profit qu'un déplacement du maximum d'intensité de fluorescence vers les plus longues longueurs d'onde est associé à un nombre croissant de noyaux aromatiques hautement substitués et/ou un nombre croissant de systèmes conjugués insaturés (e.g. **Miano and Senesi 1992**). Dans un spectre de FS, la longueur d'onde d'excitation (λ_{ex}) et la longueur d'onde d'émission (λ_{em}) sont augmentés de façon synchrone avec un intervalle constant ($\Delta\lambda = \lambda_{em} - \lambda_{ex}$). Alors, la technique synchrone consiste à varier de façon simultanée à la fois l'excitation et l'émission tout en conservant un intervalle $\Delta\lambda$ constant entre eux. Pour plus d'informations, voir les Chapitre 2 et 3.

5. Résultats et discussion

Chapitre 2 : Propriétés limnologiques des mares de thermokarst : source de gaz à effet de serre dans la toundra subarctique et arctique.

Limnological properties of thermokarst ponds: sites of greenhouse gas production in the subarctic and arctic tundra.

Les données sur les caractéristiques chimiques et limnologiques de 57 mares de thermokarst (**Tableau 1**) ont été examinées afin de dresser un portrait de ces environnements relativement peu connus. Des mares dues à des dépressions en surface d'une lithalse (pergélisol discontinu) ou d'un polygone en coins de glace (pergélisol continu) ainsi que des mares formées en périphérie des différentes formations périglaciaires ont été échantillonnées (**Figure 1**). Les mares étaient toutes peu profondes ($Z_{max} < 4.0$ m) et de faible superficie (**Tableau 2**). Cependant, beaucoup d'entre elles présentaient une stratification (**Figure 3**).

Les mares échantillonnées étaient relativement riches en éléments nutritifs par comparaison aux nombreux lacs ultra-oligotrophes présentés dans la littérature et montraient des indices d'une grande productivité hétérotrophe (en moyenne, abondance bactérienne = 5.90×10^6 cellules mL^{-1} ; productivité bactérienne = 415 pmol leucine L^{-1} h^{-}

^{1}; concentration en gaz dissous CO_2 = 1846 ppmv et CH_4 = 20 ppmv). Une corrélation, quoique faible (NH_4 : r^2 =0.62, P < 0.0001; PT (phosphore total) : r^2= 0.20, P = 0.0143) semble exister d'ailleurs entre la concentration de certains nutriments et l'abondance bactérienne (**Figure 11**). Des expériences préliminaires de limitation en nutriments ont montré des résultats contrastants pour 2 mares voisines (**Figure 12**). Une limitation en carbone dans l'une et une limitation en carbone et en phosphore dans l'autre a été observée.

Vu les grandes concentrations de dioxyde de carbone et de méthane dans la plupart des mares échantillonnés, les mares de thermokarst sont indéniablement des sources de gaz à effet de serre vers l'atmosphère (**Tableau 1**). Cependant, l'ampleur des concentrations dissoutes dans l'eau change selon le moment de la journée (**Figure 10**).

La plupart des mares étaient pauvres en solutés (conductivité moyenne de 56 µS cm^{-1}) et leur pH variait d'acide à alcalin (étendue de pH = 4.7 à 9.2). De manière générale, les sites arctiques (pergélisol continu) et subarctiques (pergélisol discontinu) présentaient de nombreuses similitudes, mais des différences considérables en ce qui a trait à la chimie de l'eau ont été observées entre les sites et à l'intérieur même d'un site donné (**Tableau 3** et **4**). Par exemple, deux mares voisines présentaient des a_{320} très différents (BGR9 : 5.8 m^{-1} et BGR10 : 26.7 m^{-1}). D'un autre côté, l'indice de fluorescence FI ne variait pas beaucoup entre toutes les mares (1.12-1.36, médiane de 1.21, moyenne de 1.22 ± 0.06; n = 50). La quantité de carbone organique variait grandement et cette différence peut vraisemblablement être attribuée à plusieurs facteurs comme les propriétés édaphiques environnantes, le type de végétation dans le bassin versant et peut-être l'âge de la mare et les communautés biologiques qui la peuplent. Les indices de fluorescence (FI) ainsi que les pentes spectrales (S) laissent croire à une source de MOD à prédominance terrestre (**Tableau 4**). D'ailleurs, la biomasse phytoplanctonique (chlorophylle *a*; **Tableau 7**) et les macrophytes, deux sources autochtones de MOD, sont peu abondants dans ce système. La forte turbidité et l'abondance apparamment élevée en zooplancton joue certainement un rôle dans le maintien d'une faible biomasse algale. Les mares qui font exception semblent présenter un mélange de MOD d'origine allochtone et autochtone. Aussi, en fluorescence synchrone, la présence d'un pic important sous les 300 nm associée dans la littérature à la MOD récente d'origine autochtone indique tout de même une certaine contribution autochtone. Certaines mares présentaient en effet des macrophytes, des plantes aquatiques

en bordure et parfois d'importantes accumulations d'algues filamenteuses. Par ailleurs, une imposante biomasse de picoautotrophes a été rapportée dans plusieurs mares de thermokarst en 2006 (**C. Dupont, pers. comm.**). Les spectres de fluorescence synchrone (**Figures 7 et 8**) montrent aussi que la MOD des mares présentent des traits communs avec ses 8 principaux pics. La différence entre les mares réside dans l'intensité des pics et l'intensité relative des pics les uns par rapport aux autres. Une revue de littérature a permis de poser des hypothèses quant à la nature des composés fluorescents attribuables à presque tous les pics observés et une certaine classification en fonction de la grosseur des molécules.

Beaucoup de mares présentaient une forte stratification. Dans les cas contraires, les conditions n'étaient pas non plus isothermales. La stratification lorsqu'elle est présente, représente une barrière pour la diffusion de nutriments et de différents composés dissous, dont les gaz. D'ailleurs, il existe des différences notables entre la surface et le fond pour plusieurs propriétés (**Tableau 6 ; Figures 3 et 8**). Par exemple, il y avait presque neuf fois plus de phosphore réactif dissous dans l'eau de fond de BGR1 par rapport à l'eau de surface. Le suivi annuel de température dans une mare près d'Umiujaq (profondeur maximale 3.2 m, taille ~300 m^2) montre une stratification presque permanente de la colonne d'eau (70% du temps, la différence de température entre la surface et le fond était >1°C) et la persistance d'eau liquide au fond de la mare tout au long de l'hiver malgré la faible taille du plan d'eau, exposant sans doute les microorganismes à des conditions physicochimiques extrêmes (**Figure 4**). Cette situation pourrait être responsable d'un flux important de CO_2 et/ou CH_4 aux périodes de mélange, au printemps et à l'automne, puisque les concentrations de gaz dissous observées étaient très élevées dans le fond des mares. Cependant, le méthane peut également s'échapper sous forme de bulles directement vers l'atmosphère en absence du couvert de glace.

Des analyses de corrélation ont permit de déterminer un lien important entre la quantité et la qualité de la MOD et la concentration en dioxyde de carbone dissous. Cela indique que la composition du sol, de la végétation et l'origine de la MOD auront un impact certain sur le potentiel de la mare à titre de source de carbone vers l'atmosphère. La MOD semble donc être un facteur clé à suivre pour mieux comprendre les flux de carbone dans ces écosystèmes. Nos résultats montrent également que les mares ayant un contenu organique élevé ont un potentiel plus élevé d'emettre des gaz à effet de serre vers l'atmosphère.

La présente étude a permis de mieux connaître les mares de thermokarst, en particulier leur productivité biologique, leur saturation en gaz à effet de serre et les mécanismes de transformation du carbone dissous montrant une dynamique relativement rapide. Ces écosystèmes méritent notre attention car ils pourraient bien tenir un rôle important dans le cycle du carbone face aux changements climatiques qui affectent présentement notre planète.

Chapitre 3 : Dégradation photochimique et microbienne de la matière organique dissoute dans les mares de thermokarst : implications pour le cycle du carbone

Microbial and photochemical degradation of dissolved organic matter in thermokarst ponds: implications for global carbon cycling.

Des expériences de dégradation photochimique et microbienne de la matière organique dissoute (MOD) ont été effectuées en 2005 sur 5 des mares qui ont fait l'objet d'une caractérisation dans le chapitre précédent. Les résultats d'une expérience préliminaire de dégradation microbienne effectuée en 2004 sur 2 mares supplémentaires sont aussi présentés. Les mares présentant différentes couleurs et turbidité avaient été choisies dans un souci de représentation d'un large éventail de propriétés optiques (**Figure 14**). Les résultats de la caractérisation de ces mares ont confirmé cette hypothèse (**Tableau 9**). Les mares présentaient un éventail de concentrations en MOD (indiqué par la concentration en COD), en MODC (exprimé par a_{320}) et en absorptivité (a_{320}/COD).

Les expériences de photodégradation ont montré qu'une fraction significative de la MOD pouvait être dégradée par la lumière naturelle dans les mares subarctiques, alors que la mare arctique présentait une dégradation largement inférieure (**Tableau 10**). La MODC ainsi que l'absorptivité ont diminué avec le temps (**Figure 16** et **17**), indiquant que la fraction chromophorique de la MOD a été préférentiellement dégradée par la lumière naturelle. De plus, le suivi des changements du spectre de fluorescence synchrone ainsi que de l'indice dérivé de celui-ci a montré que les plus grosses molécules étaient davantage dégradées (**Figure 18** et **19**). La réactivité, telle qu'estimée par la cinétique des changements dans les différentes propriétés optiques, semble différer légèrement entre les mares (**Tableau 10, Figures 16 à 25**). Une comparaison avec des données de la littérature

existante a montré un taux de dégradation comparable à d'autres écosystèmes d'eau douce. Cependant, il n'y a pas de modèle suffisamment défini qui permet de prédire la photo-réactivité d'une mare de thermokarst à partir d'un si petit échantillonnage.

Les expériences de dégradation microbienne montrent aussi qu'une fraction non négligeable de la MOD est disponible pour la communauté bactérienne (**Tableau 11**). La diminution de COD indique indirectement la transformation de COD en carbone inorganique via la respiration. Les taux de dégradation entre les mares variaient mais se retrouvaient tous dans le même ordre de grandeur sauf une (**Figure 20** à **23**). Cette mare originait de la toundra forestière et était associée à une palse boisée. Le spectre de fluorescence synchrone montrait d'ailleurs clairement une plus grande intensité relative dans les longues longueurs d'ondes pour cette mare (**Figure 15**). Les changements dans la MODC n'ont suivi aucun modèle particulier se répétant entre les mares, bien que la tendance générale était une réduction. Ces différences sont probablement en partie attribuables à la présence de différentes communautés bactériennes peuplant les mares, ces dernières dégradant différentes fractions de la MOD. Une comparaison avec des données de la littérature montre que la quantité de carbone dégradée est similaire à celle des lacs (**Tableau 11**). Qualitativement parlant, les analyses de fluorescence synchrone ont permit de déterminer que les molécules qui fluorescent dans les longueurs d'onde plus courtes (donc les plus petites molécules; **Figure 24**) et ont été préférées par les bactéries (l'indice d'humification a augmenté également; **Figure 25**). Cependant, la fluorescence a également diminué dans les moyennes et longues longueurs d'ondes. Ceci nous permet de poser l'hypothèse que les communautés bactériennes des mares thermokarstiques sont probablement bien outillées (enzymes) pour dégrader les grosses molécules dites allochtones ou terrestres.

Les taux de dégradation mesurés sont probablement sous-estimés autant en photodégradation qu'en dégradation microbienne dans les mares à forte turbidité car l'eau des expériences a été filtrée sur 0.2 µm (ce qui retire la plus grande partie de la turbidité inorganique), alors qu'une forte partie de la productivité microbienne est associée aux particules (**Tableau 8**). De plus, la présence d'argile peut théoriquement augmenter la photodégradation (**Tietjen et al. 2005;** augmentation de la diffusion de la lumière ou du chemin optique). De plus, l'interaction des deux processus de dégradation dans les eaux de surface doit sensiblement augmenter la dégradation microbienne lorsque le couvert de

glace est absent, sans oublier pendant les périodes de mélange lorsque l'eau du fond de la mare est soudainement exposée aux dégradations photochimiques. La mobilisation du carbone est favorisée localement par ces deux processus.

6. Conclusions et Perspectives

Selon l'analyse de photos aériennes datant de 1957, les mares thermokarstiques du site BGR ont pris naissance relativement récemment (60 ans et moins) (**Calmels 2005, Marchildon unpublished**). Les conditions du sol dans lesquels elles prennent naissance (minéral, tourbeux), la végétation présente (différentes écorégions), la température moyenne annuelle locale et leur âge sont certainement des facteurs qui influencent leurs caractéristiques physiques, chimiques et biologiques, ainsi que la réactivité de la MOD présente dans leurs eaux. Nous avons pu observer une grande diversité de conditions selon le site et même à l'intérieur d'un site, tant du point de vue chimique, physique que biologique. Cette variabilité s'est reflétée quand à la dynamique (cinétique) de transformation photochimique et biologique de la MOD, alors que la qualité initiale de la MOD influence la capacité des microbes à la dégrader. De plus, nous avons découvert une importante corrélation entre la quantité et la qualité de la MOD et la concentration de dioxyde de carbone retrouvée dans la mare.

Plusieurs indices prouvent que les mares thermokarstiques sont des milieux très productifs et comparable aux lacs mésotrophes à eutrophes des zones tempérées: grande abondance bactérienne, grande productivité bactérienne, haute teneur en nutriments, etc. D'ailleurs cette productivité s'est réflétée dans les concentrations en gaz dissous. Presque toutes les mares échantillonnées pour les gaz dissous étaient sursaturées par rapport à l'atmosphère. Sans nul doute, les mares thermokarstiques sont plus souvent qu'autrement des sources de gaz carbonique et de méthane vers l'atmosphère, comme la majorité des lacs étudiés dans le cadre d'une étude à grande échelle de **Cole et al. (1994)**. Par ailleurs, l'émission de méthane par les mares est probablement fortement sous-estimée lorsque le flux par bullage souvent n'est pas considéré, tel que dans notre étude. Nous avons toutefois pu observer à maintes reprises de petites bulles à la surface des mares. Le suivi des profils de température sur une période d'un an a permis de constater la présence d'une stratification pour une grande partie de la saison en absence de couvert de glace, précédé et suivi d'une période de mélange. Or, la stratification thermique est une barrière importante pour différentes composantes de la colonne d'eau, dont les gaz dissous. En effet, de plus fortes

concentrations en gaz dissous ont été mesurées au fond des mares. Ainsi, les périodes de mélange pourraient constituer d'importants apports de gaz dissous vers l'atmosphère.

L'approche expérimentale abordée pour quantifier et qualifier les processus de dégradation de la MOD dans les mares a permis de constater des taux de dégradation similaire à d'autres écosystèmes d'eau douce. Il est à noter que les taux de dégradation biologique sont probablement sous-estimés car les bactéries attachées aux particules étaient soustraites des expériences. Or, une grande quantité de mares observées en milieu subarctique présentent une forte turbidité inorganique. Les mares pourraient donc représenter des « réacteurs de carbone » et ainsi accélérer le cycle du carbone là où elles prennent naissance. De plus, la matière organique qui demeure récalcitrante aux transformations se retrouvera éventuellement dans le bassin de drainage vers l'océan, où l'apport de nouvelle MOD terrestre a des impacts divers sur les bilans de température et de lumière qui façonnent littéralement le réseau alimentaire microbien dans les zones côtières de l'océan.

La fonte du pergélisol, qui permet la mobilisation de la matière organique qui y était stockée, amène beaucoup d'interrogations. Puisque des changements importants du climat affectent présentement les régions nordiques et que le pergélisol occupe une grande partie du paysage, la formation de mares par des processus thermokarstiques est un phénomène préoccupant. Ces mares feront-elles une différence dans les bilans de carbone des milieux nordiques? Bien que ces mares semblent en progression, la recolonisation par les plantes peut inverser les flux de carbone. L'augmentation de température, poussant toujours plus au nord la limite de la végétation permettra-t-elle de compenser l'augmentation des émissions dues à la formation de mares thermokarstiques? Nous espérons avoir apporté quelques éléments de réponse qui permettront aux futures études d'être mieux outillées pour répondre aux nombreuses questions qui demeurent. Quelle est la durée de vie d'une mare de thermokarst? La couleur des mares est-elle liée à son âge? Combien de carbone est libéré durant sa vie? Le carbone libéré provient-il surtout de la tourbe en décomposition ou de la végétation croissant en bordure? Quelle est l'importance des flux de méthane par bullage? Quels sont les liens entre la flore microbienne des mares, leur stucture thermique, la qualité de la MOD et leur production de gaz?

Deuxième partie

Les articles

CHAPITRE 2: Limnological properties of thermokarst ponds: sites of greenhouse gas production in the subarctic and arctic tundra. (*Propriétés limnologiques des mares de thermokarst: source de gaz à effet de serre dans la toundra subarctique et arctique*)

Résumé

Les données sur les caractéristiques chimiques et limnologiques de 57 mares de thermokarst ont été examinées afin de dresser un portrait de ces environnements relativement peu connus. Les mares échantillonnées étaient toutes peu profondes (Z_{max} < 4.0 m), de petites superficies (< 525 m^2), riches en éléments nutritifs (e.g., valeur minimale de 6.2 µg L^{-1} en phosphore total, moyenne = 50 µg P L^{-1}; valeur moyenne NH_4 de 91 µg N L^{-1}) et recelaient des indices d'une grande productivité hétérotrophique (abondance bactérienne = 5.9 $\times 10^6$ cellules mL^{-1}; production bactérienne = 415 pmole leucine L^{-1} h^{-1}; concentration en gaz dissous CO_2 = 1846 ppmv et CH_4 = 20 ppmv). Une grande partie de la productivité bactérienne était d'ailleurs associée aux particules (> 3 µm) dans les mares où cette mesure a été prise (>56% ; n =2). La plupart des mares étaient pauvres en solutés (conductivité moyenne de 56 µS cm^{-1}) et leur pH variait d'acide à alcalin (étendue de pH = 4.7 à 9.2). Les fortes concentrations en gaz dissous laissent croire que la majorité des mares thermokarstiques sont des sources de carbone pour l'atmosphère. La concentration en CO_2 dissous était liée à la quantité et la qualité de la matière organique dissoute (MOD). Plusieurs mares présentaient une stratification au moment de l'échantillonnage et un suivi à long terme de la température a permis de constater que le fond de la mare demeure liquide durant tout l'hiver et que la colonne d'eau demeure stratifiée une grande partie de l'année (71 % du temps). D'ailleurs, des différences importantes pour plusieurs variables entre la surface et le fond ont été observées durant l'été. Ainsi, la saison de mélange apporte sans doute de grands changements physicochimiques avec ses conséquences pour le biota. Les concentrations en gaz dissous dans le fond des mares étaient beaucoup plus importantes (4 à 10 fois plus de CO_2 et 2 à 125 fois plus de CH_4) que dans l'eau de surface. Les mares thermokarstiques seraient donc des sources de carbone plus importantes aux saisons de mélange (printemps et automne).

Abstract

Chemical and limnological data gathered from 57 thermokarst ponds were examined to describe these relatively unknown environments. All sampled ponds were shallow (Z_{max} < 4.0 m), with small surfaces/area (< 525 m^2), high content in nutrients (e.g., minimum concentration of total phosphorus 6.2 µg L^{-1} , mean=50 µg P L^{-1}; mean NH_4= 91 µg N L^{-1}) and showed indices of high heterotrophic productivity (microbial abundance = 5.9 $\times 10^6$ cells mL^{-1}; bacterial production = 415 pmole leucine L^{-1} h^{-1}; dissolved gas concentration of CO_2 = 1846 ppmv and CH_4 = 20 ppmv). An important fraction of bacterial production was associated with suspended particles (> 3 µm) when this measure was taken (>56%; n =2). Most of the ponds were low in ions (mean conductivity 56 µS cm^{-1}) and slightly acidic to alkaline (pH range = 4.7 to 9.2). The CO_2 concentration in water was related to both the quantity and quality of dissolved organic matter (DOM). High concentrations in dissolved gases (CO_2 and CH_4) make us believe that these ponds represent a carbon source to the atmosphere. Several ponds were stratified when sampled and long-term monitoring showed that water at bottom of the pond did not freeze in winter and the water column remained stratified 71% of the time. A difference has been observed between surface and bottom waters in summer time. Then, mixing in spring and autumn likely brings great physicochemical changes with important consequences on the biota. Concentrations of dissolved gases were much higher in bottom waters than at the surface (4 to 10 times more CO_2 and 2 to 125 times more CH_4). Thermokarst ponds seem to be a more important source of carbon to the atmosphere at period of mixing.

Introduction

Permafrost, which is defined as soil that remains below 0°C for two or more years (**Harris et al. 1988**), is estimated to occupy about 24% of the northern hemisphere land surface (**Zhang et al. 1999**). In Canada, permafrost represents about 43% of the total area (approximately 25% in Quebec). The term thermokarst refers to characteristic landforms which result from thawing of ice-rich permafrost or the melting of solid ice. Thermokarst occurs extensively in arctic and subarctic areas. It is characterised by an irregular hummocky topography, where irregular pits and depressions develop by thaw settling in an otherwise smooth topography (**Brown and Grave 1979**; **Hinzman et al. 1991**). The important processes involved in thermokarst formation include thaw, ponding, surface and subsurface drainage, surface subsidence and erosion (**Yoshikawa & Hinzman 2003**). Even small surface irregularities and slight temperature increase can start thermokarst processes and create thermokarst ponds. Water initially pools in a depression and its presence begins to thaw the permafrost beneath. As thawing continues along pond margins, the pond extends. Thaw extension continues until higher ground is breached, interconnecting different ponds and eventually creating an outlet channel. Once the permafrost completely thaws under a pond, an open talik (patch of unfrozen ground in an area of permafrost) forms and the surface-water system directly connects to a sub- or intra-permafrost aquifer. As a result, pond water starts draining, resulting in a declining water surface (**Yoshikawa and Hinzman 2003**). However, in the discontinuous permafrost area, the BGR site is underlain by post-glacial marine silts (same site as **Calmels and Allard 2004**), which render the soil impermeable the soil below the ponds. As a result, the ponds remain even after the permafrost has completely disappeared, unless the vegetation recolonizes the system and the aquatic state recedes.

With different types of permafrost are associated different morphologies of ponds (**Figure 1**). In continuous permafrost area, the ponds develop in depressed polygons and channels left by melted ice-wedges (**Lachenbruch 1962**; **French 1976; Billings and Peterson 1980; Mackay 1990**), while in discontinuous permafrost area, ponds develop either on the depressed top or in the periphery of an isolated palsas or lithalsas (mineral palsas). Palsas are mounds with a permanently frozen peat and mineral soil core. They typically rise to a height of 0.5–10 m above the mire surface within the discontinuous

permafrost zone (**Åhman 1977**; **Seppälä 1986, 1988**). Palsas normally demarcate the outer limit of permafrost (**Zoltai 1971**; **Seppälä 1988**; **Sollid and Sørbel 1998**). The formation of a palsa was well explained by **Seppäla (1986)**. Lithalsas are comparable in dimension to palsas but they develop principally on soil with high content of silt and clay, where the peat cover is absent.

An increase in permafrost temperatures has been observed in northwest Canada, Siberia, northern Europe and in Alaska during the last 20 years (**Richter-Menge et al. (NOAA) 2006 and references therein**). The amount of soil warming differed among locations, but it was typically 0.5–2°C at the depth where there is no seasonal temperature variation in permafrost. However, these data also indicate that the increase in permafrost temperatures is not monotonic. During the observational period, relative cooling has occurred (**Richter-Menge et al. (NOAA) 2006**). Recently, thawing of permafrost and formation of thermokarst has been reported both in Europe (**Thorhallsdottir 1994**; **Matthews et al. 1997**; **Sollid and Sórbel 1998**; **Zuidhoff and Kolstrup 2000**; **Zuidhoff 2002**; **Luöto and Seppälä 2003**; **Christensen et al. 2004**; **Smith et al. 2005**) and North America (**Laprise and Payette 1988; Laberge et Payette 1995**; **Osterkamp and Romanovsky 1999; Osterkamp et al. 2000**; **Beilman et al. 2001**; **Nelson et al. 2001**; **Payette et al. 2004**; **Jorgenson et al. 2006**). For example, the phenomenon was observed in a subarctic peatland by **Payette et al. (2004)** over the past 50 years, where surface area occupied by ponds increased as the permafrost melted. This has also been observed at a site located closer to the Hudson Bay (**Calmels 2005**). On the other hand, in some areas in Alaska, shrinking of pond surface areas has been observed (**Yoshikawa and Hinzman 2003)** resulting in a talik formation. This apparent contradiction can be explained if the phenomenon is considered as a continuum, where initial permafrost warming leads to development of thermokarst features and lake expansion, followed by lake drainage as the permafrost degrades further (**Smith et al. 2005**). Exceptions to this conceptual model surely exist and might depend on specific soil geomorphology.

Future increases in regional temperature are expected to cause widespread degradation of permafrost, particularly in the zone of discontinuous permafrost where ground temperatures are close to the freezing point (**IPCC 2007**). **Woo et al. (1992)** estimated that a warming of 4-5 °C could lead to a 50% reduction in the area underlain by discontinuous permafrost in arctic and subarctic Canada. More recently, **Lawrence and**

Slater (2005) used a fully coupled global climate model CCSM3 (Community Climate System Model, version 3) to examine current distribution and future projections of permafrost with explicit treatment of frozen soil processes. Their simulated present-day permafrost in the model agreed well with observational estimates- 10.5 million km^2, excluding ice sheets. They estimated that by 2100, as little as 1.0 million km^2 of near-surface permafrost will remain. However, their results have been debated (**Burn and Nelson 2006**).

These changes in permafrost regime will certainly have a great impact on carbon cycling in high latitude environment. **Zimov et al. (2006)** pointed out that permafrost is a large carbon reservoir that is rarely incorporated into analyses of changes in global carbon reservoirs. They estimate the carbon reservoir in frozen yedoma (frozen loess that was deposited during the glacial age, covering more than 1 million km^2 of the north plains of Siberia and Central Alaska to an average depth of ~25 m) to be ~500 Gt in Siberia. Such estimates are more uncertain concerning North America, but the carbon content is undoubtedly high, probably ranging from 60 to 190 Pg (**Hobbie et al. 2000**).

Among studies exploring permafrost disturbances, several have focused on hydrological regimes, geophysical profiling and groundwater dynamics in permafrost areas (**e.g. McNamara et al. 1998**; **Schwarmborn et al. 2002**; **Yoshikawa & Hinzman 2003**). For example, **Yoshikawa & Hinzman (2003)** characterized groundwater infiltration and surface water dynamics for a tundra terrain located in discontinuous permafrost. Other studies explored the effect of permafrost degradation on vegetation (e.g. **Jorgenson et al. 2001**; **Lloyd et al. 2003**). **Chapin et al. (2000)** noted that changes in thermokarst and the aerial extent of wetlands, lakes and ponds would alter gas fluxes. They observed the notable discrepancies in estimates for the size and direction of CO_2 fluxes between high latitude ecosystems and the atmosphere. **Walter et al. (2006)** observed an increase of emissions of 58 percent in northern Siberia cause by the expansion of thaw lakes between 1974 and 2000. Furthermore, the Pleistocene age (35,260–42,900 years) of methane emitted from hotspots along thawing lake margins indicates that this positive feedback to climate warming has led to the release of old carbon stocks previously stored in permafrost.

To our knowledge, very few studies have characterized thermokarst ponds themselves during their lifetime and the implications of their formation and duration on ecosystem processes and carbon cycling.

Even small changes in regional conditions could be detectable by studying thermokarst processes. We know that the permafrost represents a large part of the arctic and subarctic landscape. Therefore, thermokarst landforms and ponds can be useful indicators of global warming. Melting of permafrost may induce feedback mechanisms such as the activation of the soil carbon pool and a northward expansion of shrubs and forests (**Lawrence and Slater 2005**). The present study was undertaken as a part of a broader program to examine the evolution of this overlooked ecosystem with regard to recent climatic changes and to improve the understanding of the role of permafrost degradation on the global carbon cycle. Our objectives were to measure the physical, chemical and biological properties of thermokarst ponds situated in different sites and latitudes and to link these properties with their potential to act as a source of carbon to the atmosphere. Experiments on the reactivity of DOM were also performed to study the fate of dissolved organic matter in the ponds. This work is presented in **Chapter 3.** This study should provide reference data for future studies on thermokarst ponds.

Material and Methods

An extensive study was carried out during July and August 2004 and 2005 in Nunavik (discontinuous permafrost; near Whapmagoostui-Kuujjuarapik N55°16' W77°46', Boniface River N57°45' W76°20',Umiujaq N56°32', W76°31' and Boutin River N55°49' W76°34') and on Bylot Island in Nunavut (continuous permafrost; N73°09' W79°58') (**Figure 2**). Six additional ponds were sampled during the Amundsen cruise in September 2004 (near Umiujaq, Kangiqsualujjuaq N58°41' W65°56' and Whapmagoostui-Kuujjuarapik). Mean annual temperature at Kuujjuarapik is -4.4°C with a mean July temperature of 10.6°C and a mean January temperature of -23.4°C. Mean annual temperature at Inukjuaq (near Boniface river) is -7°C with a mean July temperature of 9.4°C and a mean January temperature of -24.8°C. Mean annual temperature at Pond Inlet (near Bylot Island) is -15.1°C with a mean July temperature of 6°C and a mean January temperature of -32.4°C (**Environment Canada, 2000**). Abbreviations for all sites are available in **Table 1**. A detailed description of the sites is available in **Delisle et**

al. (2003) and **Calmels and Allard (2004)** for the Umiujaq site (BGR), and in **Arlen-Pouliet and Bhiry (2005)** for the Whapmagoostui-Kuujjuarapik site (KUJ). There is no existing description of the KWK (about 18 km north of KUJ site), BOU (about 100 km north of KUJ site) and KAN sites. Our sampling site close to Boniface River (BON) was in the same region described in **Payette and Delwaide (2000).** A location map and geographic features of Bylot Island are available in **Vézina and Vincent (1997)** and **Fortier and Allard (2004).** Vegetation zones (ecoregions) and local dominant vegetation are indicated in **Table 1.** Vegetation is dominated at BYL sites by sedges (e.g., *Carex aquatilis* var. *stans*, *Eriophorum scheuchzeri*), grasses (e.g., *Arctagrostis latifolium*, *Dupontia fischeri*, *Pleuropogon sabinei*) and fen mosses (e.g., *Drepanocladus* spp., *Aulocomnium* spp.; **Ellis and Rochefort 2006**). The site presents a thick peat cover and shelters important bird colonies enriching the ponds. In subarctic sites, dominant vegetations are shrub and trees. The distribution of permafrost is available for some of our study sites in Northern Quebec in **Lévesque et al. (1988)**. We observed the ponds to be in most cases disconnected in discontinuous area (but they can merge into bigger ponds) whereas there were many connections between ice-wedge ponds in the continuous permafrost area.

Soil from BGR site has been previously analyzed for sediment description, ice and gas content. Soil essentially contains clays and silts with a low content in organic matter (<1.5%). The site was representative of the region (**Calmels and Allard 2004**). This is principally a field of lithalsas, but some permafrost mounds presented a peat cover (**Figure 1 c.** an arrow indicates the presence of peat). The vegetation was mainly growing between the mounds, and ostioles were present on the top of many lithalsas. The absence of permafrost between lithalsas has been widely documented in this region (**Payette and Seguin 1979**; **Lagarec 1980; Seguin and Allard 1984**; **Allard and Seguin 1987**). At the KWK site, the mounds appeared essentially mineral but few of them were still apparent (permafrost has melted) and the vegetation has densely colonised the site (**Figure 1 a.**). At BON, KUJ and BYL sites, an important peat cover was present (at KUJ, 2.70 meter thick; **Arlen-Pouliet and Bhiry 2005**) (**Figure 1 b., d., e.**).

Ponds were sampled in a way to represent the different colors, development phases and humification degrees. A total of 57 thermokarst ponds in addition to 15 representative

surrounding aquatic environments (5 standard ponds, 4 puddles with sphagnum, 3 rivers and 2 lakes; **Table 2**) were sampled for DOC content, total bacterial abundance, total suspended solids (TSS) and DOM optical characteristics (CDOM absorbance and fluorescence; see below). Five of the ponds (named principal ponds hereafter) were studied more extensively, including bathymetry, surface area, and profiles of physicochemistry, nutrients, phytoplanktonic pigments, planktonic bacteria and bacterial production. It is in these ponds where microbial and photochemical degradation experiments were performed. These results will be presented in Chapter 3.

Physical environmental variables

We used a weighted calibrated line to measure the maximum depth of most ponds. In four ponds, we took manually several depth measurements to approximate their bathymetry. At each 3 meters approximately, transects were performed along which 3 depths were measured. Width and length were also measured. From these measurements, the area and volume of each pond was approximated.

Temperature (+/- 0.15 °C), conductivity (+/- 0.5%), dissolved oxygen (+/- 0.2 mg/L) and pH (+/- 0.2) were recorded in situ on a 600R multiparametric probe (YSI Incorporated) in 2005, whereas temperature, dissolved oxygen and pH were measured with an Idronaut probe in 2004. Measurements were taken between 10 and 16h. Conductivity and pH probes were calibrated once a week whereas dissolved oxygen probe was calibrated once a day. Profiles were obtained by starting at the lake surface and taking data readings at 0.25 m intervals.

We also monitored the temperature at the surface (0.3 m) and near-bottom (2.75 m; maximal pond depth 3.2 m) in one of the five principal ponds during an entire year (July 2005 through July 2006) using thermistors (HOBOware™, Onset Computer Corporation).

Chemical variables

Suspended solids of subsurface water samples were collected on 25 mm glass-fiber filter (MFS, Advantec) that has been pre-combusted and pre-weighed. A volume of 12 to 925

mL was filtered to collect as much material as possible before clogging, the filters were kept frozen until analysis. Filters were dried at 60°C (approximately two hours per cycle) and weighed until they reached a constant weight. The filters were then burned for 2 h at 500°C. The volatilized solids are considered a rough estimation of the organic fraction in suspended solids. What remained on the filter is consider fixed or an approximate of the inorganic portion. We calculated a ratio of volatile/fixed solids to estimate the contribution of organic material to the turbidity.

Subsurface water samples were collected (10-30 cm). Samples were analyzed for: total phosphorus (TP), soluble reactive phosphate (SRP), total nitrogen (TN), nitrate (NO_3) and ammonia (NH_4). Within 6 h of sampling, the water for SRP and NH_4 was filtered through cellulose acetate filters (pre-rinsed with ultrapure water and pond water; MFS Advantec), transferred into 140 mL pre-washed Teflon-capped glass bottles with 0.7 mL of H_2SO_4 30%. We added 0.8 mL of H_2SO_4 30% to unfiltered water for determination of TN and TP. All samples were preserved at 4°C until analysis, within 6 weeks. SRP (QuikChem® Method 10-115-01-1-B) and NH_4 (QuikChem® Method 10-107-06-2-B) were both determined by flow injection analysis (Lachat Instruments). TP was determined after perchlorate digestion and a manual spectrophotometric measurent using a 10 cm-cuvette as in **Stainton et al. (1977)**. TN was determined by flow injection analysis. How long between sampling and analysis, how preserved?

DOM characterization

Water samples for the determination of DOC content and optical characteristics were filtered through 0.2 μm sterile cellulose acetate filters pre-rinsed with ultrapure water and pond water. Samples were stored at 4°C in the dark until analysis. Spectroscopic measurements were run at natural pH and at room temperature. DOC concentrations were measured using a Shimadzu TOC-5000A carbon analyzer calibrated with potassium biphtalate (non purgeable organic carbon method COD 410.2).

To determine the chromophoric fraction of DOM (CDOM), absorbance scans over the wavelength range of 250-800 nm were performed on a spectrophotometer (Cary 100 UV-VIS, Varian) at natural pH using a 1 cm acid-cleaned quartz cuvette on dual beam mode, at a speed of 240 nm min^{-1} with slit width of 2 nm. Absorbance was measured against ultrapure water that was changed every 10 scans. Absorption coefficients were calculated

as $\mathbf{a(\lambda)= 2.303 \times A(\lambda)/l}$, where $\mathbf{a(\lambda)}$ is the absorption coefficient at wavelength λ, A_λ is the absorbance at wavelength λ and **l** is the pathlength of the cuvette (m). The spectral behaviour of $a(\lambda)$ can be modelled by the equation:

$$a(\lambda) = a(\lambda_0)\, e^{S(\lambda_0 - \lambda)}$$

Spectral slope coefficients (S) were calculated as in **Mitchell et al. (2002)** using an exponential fit.

Synchronous fluorescence (SF) spectra were recorded over the excitation wavelength range 200-700 nm at a scan speed of 120 nm min^{-1} using a spectrofluorometer (Cary Eclipse, Varian) in the synchronous mode with a slit of 5 nm on both sides and a wavelength differences between the excitation and emission beams of 14 nm as in **Belzile et al. (2002).** This setting minimizes the overlap between CDOM peaks and the Raman water peak and greatly suppressed the latter. Data were corrected for the inner-filter effect (**Mobed et al. 1996**) according to **McKnight et al. (2001)**, except that the absorption coefficient of the sample was measured by spectrophotometry (as described above). The blank was then subtracted from the corrected data. Data were smoothed to eliminate noise with a second order polynomial (**Sigma Plot 8.0**). A humification index was determined as proposed in **Kalbitz et al. (1999)**, where the quotient of fluorescence intensity at 400 and 360 nm (humification index-1: HI-1) or at 470 and 360 nm (HI-2) is considered a measure of polycondensation and humification degree. Increasing quotients of fluorescence intensity indicates a higher degree of polycondensation and of humification.

In addition, emission scans of fluorescence were taken with the same spectrofluorimeter as described above but with a fixed excitation wavelength at 370 nm. The intensity of fluorescence was measured from 400 to 700 nm, at the speed of 240 nm^{-1} with a 5 nm slit width. Data were corrected for the inner-filter effect (as described above for SF) to further determine the fluorescence index (FI). The FI was developed by **McKnight et al. (2001)** as a simplified approach to characterize the source of the fulvic acid fraction of DOM. This is the ratio of the emission intensity at a emission wavelength of 450 nm to that at 500 nm. The FI characterizes the slope of an emission curve at an excitation wavelength of 370 nm. The peak emission intensity occurs at a lower wavelength in samples in which the DOM is microbially derived (forward left) than the samples originating from plant and soil of the landscape (forward right).

Dissolved gases (CH_4 and CO_2)

The method most commonly used for direct quantification of the concentration of gas in water is equilibration of a water sample with a small headspace and measurement of the partial pressure of gases in this headspace **(e.g. Hesslein et al. 1990; Algesten et al. 2004)**. The concentration of CO_2 and CH_4 in the headspace and a simultaneous recording of water temperature are then used to calculate the aqueous gas concentrations by means of Henry's Law.

We measured dissolved CO_2 and CH_4 at the surface of all ponds and at the bottom of four ponds. The system consist of a 2L Nalgene bottle with a bottom outlet connected to a 5 mL syringe and closed on top with Nalgene stopper, pierced with a double-end needle (Vacutainer needles, 20 gauge). The bottle was filled with pond water, 20 mL of water were removed from the bottle into syringe (20 mL headspace filled with ambient air), the needle was closed with a small stopper and the bottle shaken for three minutes to achieve equilibrium between the gas phase and the water phase in the headspace. After equilibration, the gas phase was sampled in duplicate 3 mL vials (pushing 5 mL of water from the syringe back into bottle) previously flushed with helium and emptied down to ~100 atm. The vial's rubber stoppers were previously baked for 6h at 60 °C to eliminate any methane contamination. The samples were analysed within 9 weeks by gas chromatography (VARIAN 3800 with COMBI PAL Head Space injection system and CP-Poraplot Q column). The same system was used to estimate the daily variation of gas concentrations in 3 ponds taking gas samples during at least 26 hours at given intervals.

Biological components

Subsurface samples were collected in Nalgene bottles for determination of Chlorophyll *a* concentration and bacterial abundance, at least 0.60 m from the margin of the ponds. The water samples were filtered through glass-fibre filters (grade GF/F, MFS Advantec), within 6 hours of sampling depending on logistical constraints. The filters were kept frozen (-20 °C at the field laboratory and -80 °C in the central laboratory, except during transport, where they were kept frozen with ice packs at approximately -5°C) until the extraction. Chlorophyll *a* (Chl *a*) was subsequently determined by high pressure liquid chromatography (HPLC) by the method described in **Zapata et al. (2000)**.

We estimated the abundance of pelagic bacteria in all ponds and surrounding area and the bacterial production in four ponds. Subsamples of water were fixed with a filtered solution of paraformaldehyde (1% final concentration) and kept at 4 °C. The bacteria were stained during 2 minutes at room temperature with DAPI (4',6-diamidino-2-phenylindole, DNA probe, **Sigma**) at a final concentration of 5 $\mu g\ L^{-1}$. The samples were diluted if necessary in order to obtain a concentration of 30-75 bacteria per microscope field to facilitate the count. Samples were then filtered onto black polycarbonate filters (0.22 µm, Nuclepore) for epifluorescence inverse microscopy (1000×; Zeiss Axiovert) (method inspired from **Porter et al. 1980** and **Kemp et al. 1993**).

Heterotrophic prokaryote production was determined in 13 ponds from the BGR and KWK sites. The ^{3}H-leucine (^{3}H-Leu) incorporation method was used as a measurement of protein synthesis by heterotrophic picoplankton (Bacteria and Archaea; hereafter the word 'bacteria' includes both Archea and Bacteria because they cannot be distinguished with this method). The water was fractionated with 3 µm polycarbonate filters (47 mm, Poretics) to obtain the production from free living bacteria and bacteria attached to particules. The filters were previously flushed with sample water and were changed whenever clogging was apparent. For each measurement, 5 sterile microvials (2 mL) received 1.25 mL of water sample; 2 of them were killed with trichloroacetic acid (TCA; 5% final conc.) to serve as controls. The microvials were then inoculated with ^{3}H-Leu (specific activity: 167 Ci $mmol^{-1}$, Amersham Biosciences). Because it was not possible to get the results of saturation curve while on the field (to determine the proper concentration of ^{3}H-Leu for this specific community), we used a standard final concentration of 10 nM as proposed by **Simon and Azam (1989)**. Microvials were incubated in the dark at simulated in situ temperature for 2 h. Differences to actual in situ temperature were generally less than 2°C. Protein synthesis was stopped by the addition of TCA (5% final conc.). The microvials were then stored at 4°C to be processed in the next 24 h (see below) or frozen (-20°C) to be processed back at the laboratory.

To eliminate unlabelled ^{3}H-Leu, a microcentrifugation protocol was followed, modified from **Smith and Azam (1992).** After a first centrifugation step (12 min, 13 000 rpm), supernatant was aspirated with a Pasteur pipette connected to a vacuum pump. Care was taken not to aspirate the pellet and to aspirate all remaining supernatant drops. The pellet

was rinsed by adding 1 mL of TCA 5% followed by a second centrifugation round. Supernatant was aspired and microvials stored at -20°C. The microvials received 1 mL of scintillation liquid (OptiPhase 'HiSafe' 2; Wallac Scintillation products) and were then vortexed. After 24 h at ambient temperature, samples were radio-assayed in a Beckman LS 6500 scintillation system.

The equation used to transform DPM in rate of leucine incorporation per volume (mmol Leu L-1 h-1) was:

$$\textbf{mmol Leu L}^{-1}\textbf{ h}^{-1} = \frac{(\text{dpm sample} - \text{dpm blank}) * 4.5 \times 10^{-13}}{SA * t * V}$$

Where dpm is disintegrations per minute, 4.5×10^{-13} is a constant representing the number of Curies (Ci) per dpm, SA is 3H-Leu specific activity in Ci $mmol^{-1}$, t is incubation length in hours and V is incubation volume in liters.

Saturation curve and temporal series experiments showed that ^{3}H-Leu incorporation was linear for at least 300 min and that 10 nM was far from saturating bacterial uptake of ^{3}H-Leu (annex 3). Thus, our bacterial production calculations should be considered as conservative estimates of actual production rates.

Enrichments experiments were performed in two ponds (BGR1, BGR5) to estimate the limitation of thermokarst pond bacterial communities in nutrients and carbon. For this, twelve polycarbonate bottles (Nalgene, 1L) were filled with bulk (unfiltered) water after being thoroughly rinsed with the sample. Three bottles were kept unenriched, three received 5 µM of glucose (final conc.), three received 5 µg of phosphorus (as K_2HPO_4; final conc.) and 3 received both glucose and phosphorus. Bottles were incubated in the dark at simulated *in situ* temperature for 24 h. At the end of incubation, bacterial production was measured in each bottle.

Results

Physicochemical and environmental characteristics

Most of the sampled ponds were surrounded by bog vegetation and *Sphagnum* mosses were widely present in their watershed, mostly in their periphery. Shrubs and trees were also present around the subarctic ponds. Sites presented similar characteristics although

some particularities. On a small scale, we observed relatively large differences in limnological properties, for example, a DOC of 2.7 mg C L^{-1} versus 5.1 mg C L^{-1} in two neighbouring ponds (distance by less than 50 m; BGR1 and BGR10, **Table 3**) and with apparently the same vegetation surrounding both of them. The presence of trees or shrubs marked an evident contrast in subarctic sites compared to arctic sites. In addition, among subarctic sites, we observed differences in densities of vegetation. Vegetation was quite dispersed at the BGR sites, whereas dense shrubs were present at the KWK and KUJ sites. In contrast to other subarctic sites, trees were more abundant than shrubs at the BON site. The sampled ponds encompassed a wide range of limnological conditions, as presented in **Table 1, 3,** and **4**.

Ponds were deeper in Nunavik (BGR, KWK, BON sites; depth range of 0.40 to 3.50 m, average 1.95 m, n = 16; if only ponds on lithalsas are considered: 1.00-3.50 m, average 2.30 m, n = 13) than in Nunavut (BYL site; maximum estimates 0.90 m). Results for bathymetry soundings of the principal ponds (all originated from a depression) are shown in **Table 5**. The morphometry was relatively regular (more or less circular) in the majority of the ponds originating from a depression of a lithalsa, unless two or more ponds merged or when the pond was at a young stage of formation. The same pattern was observed for depressed polygons in continuous permafrost area. On the other hand, channels originating from melting of ice wedges in continuous permafrost showed irregular shapes.

Surface water temperature at time of sampling varied from 7 to 21°C with an average of 14 ± 4.2 °C **in 2004**, and from 7 to 28°C with an average of 15.8 ± 6.7 °C **in 2005.** Several ponds were thermally stratified (**Figure 3;** e.g., ponds at the BGR and KWK sites), predominantly the ponds formed on depressed lithalsas. In ponds of the forested tundra (e.g., BON site) in discontinuous permafrost, and ponds in continuous permafrost (e.g. BYL site), a thermocline did not develop, but the conditions were not isothermal. Even one of the shallower ponds in forest tundra (BON 1) showed a difference of 2°C between surface water and bottom water at 40 cm of depth (**Figure 3 f.**). These are most likely short term (or diurnal) stratification features. The stratification observed in the summer 2004 was stronger than in 2005 (weather data not available when printed. Profiles are available in one BGR pond sampled during both years. They showed distinctive profiles but similar patterns (**Figure 3 a.** and **b.**). Temperature and percentage

of dissolved oxygen (DO) decreased with depth with an abrupt change below the thermocline in stratified ponds. On the other hand, the pH remained relatively stable in the whole water column (not shown). In almost all stratified ponds, the bottom water was hypoxic (**2004**: 5-31%, 0.5-4.1 mg O_2 L^{-1}; **2005**: 1-13%, 0.1-1.4 mg L^{-1}; **Figure 3** and **Table 6**). However, some ponds presented a thermal stratification but high DO in bottom waters (see **Table 6**; BGR9 and BGR10). Also, some ponds showed a peak in DO at varying depths in the water column, followed by a rapid decrease and a hypoxic hypolimnion. In BGR1, the extinction coefficient showed that the DO peak was situated in the photic zone (0.5 m). In some of the shallower ponds in Nunavut, which presented weaker stratification, there was still an important DO gradient (45-55% DO, 5.3-6.8 mg O_2 L^{-1} in bottom waters compared to saturation at the surface).

Conductivity varied a lot among ponds, averaging 52.5 ± 50.5 µS cm^{-1}, and was significantly higher in arctic ponds with 89.73 ± 58.50 µS cm^{-1} as compared to subarctic with 39.45 ± 43.03 µS cm^{-1} (**Mann-Whitney, P < 0.001**). All other variables were not statistically different from each other. Monitoring of the surface (0.3 m) and bottom (2.75 m) water temperature of the pond BGR1 (z_{max} around 3.20 m; N56°36.654 W76°12.924) showed that the difference in temperature between the two depths was > 1°C, 71 % of the year (**Figure 4 a.**). This pond had an ice cover from approximately the end of November to the end of April, with two principal periods of mixing in early summer (**Figure 4 c.**) and autumn. At some point we observed other isolated mixing events with short-term stratification (**Figure 4 b**). The bottom water remained liquid during the whole winter at a temperature of around 1-3°C.

Many ponds were highly turbid. Results showed a wide range of TSS concentrations in surface waters (**Table 4;** 0.4 to 271 mg L^{-1}; average = 20 ± 52 mg L^{-1}; n = 37), but only two ponds presented values higher than 150 mg L^{-1}. Values from bottom waters ranged from 29 to 303 mg L^{-1} (average = 144 ± 126 mg L^{-1}; n = 4) and were significantly higher than at the surface (**Mann-Whitney, P = 0.004**). The ponds in BGR and KWK sites (originating from lithalsas) had significantly higher TSS values than did ponds from the other sites (**Mann-Whitney, P < 0.001**). The ratio of volatile/fixed solids (annex 4) was always higher than 1 at the BON and KUJ sites, and less than 1 at the BGR and KWK sites (except KWK9). At the BYL site, ratio was generally ≤1, but there were some exceptions >1 (5 out of 14). A ratio > 1 roughly indicates that TSS is mostly composed of

organic material, likely originating from zooplanktonic organisms (organisms themselves, exudates, "sloppy feeding") that were observed in high abundance in the ponds. On the other hand, a ratio <1 indicates the predominance of inorganic particulates, likely silts and clays that confer the characteristic milky appearance of many ponds. We observed a positive correlation between TSS and the concentration of TP in ponds where the two variables were available (**Figure 5**). Estimates of vertical extinction coefficient (Kd_{PAR}) of visible light (photosynthetic available radiation or PAR) are available for some ponds sampled in 2004, all values being relatively high (estimates: 2-28 m^{-1}; avg = 9.1 ± 8.2 m^{-1}), but no correlation was found between TSS and this coefficient.

Most nutrients in thermokarst po nds were higher than what is generally observed in lakes of the region. Ammonium (NH_4) concentrations averaged 91.0 ± 58.4 µg N L^{-1} (n = 30), nitrates (NO_3) 176 ± 315 µg N L^{-1} (n = 30), total phosphorus 50.0 ± 49.8 µg P L^{-1} (n = 29), soluble reactive phosphorus (PO_4) 15.4 ± 49.6 (n = 31). TN was below detection limit (<0.3 mg N L^{-1}), except in two ice wedge ponds, BYL2 (surface water = 0.4 mg N L^{-1}) and BYL11 (surface water = 0.4 mg N L^{-1}; bottom = 9.2 mg N L^{-1}. However, the concentration of nitrates (NO_3) was always higher than the range generally found in Arctic lakes (**Pienitz et al., 1997; Lim et al. 2001**). Two measurements of TP in bottom waters showed higher (up to 3.7 times) concentrations compared to surface waters. All measurement for bottom waters are available in **Table 6**.

DOM characterization

DOC presented a wide range of values (**Table 3;** 1.3 – 26.0 mg L^{-1}) and did not differ significantly between arctic and subarctic sites, with an average of 8.8 ± 5.7 mg L^{-1}. We observed a difference between DOC concentrations in ponds with forested or shrub watersheds (i.e. higher values in BON and KWK ponds as compared to BGR ponds). BGR1 and BGR5 sampled in 2004 and 2005, showed a variation of DOC through time (BGR1, 3.3 and 2.5 mg L^{-1}; BGR5, 1.3 and 4.7 mg L^{-1}, respectively in 2004 and 2005). These ponds were also sampled in 2006, showing again different values (2.6 and 3.1, respectively in BGR1 and BGR5; **Laurion unpublished**). To quantify the chromophoric portion of DOM (CDOM), the absorption of CDOM at 320 nm was used (a_{320}; **Table 3**). Values of the entire data set ranged from a minimum of 3.1 to a maximum of 179 m^{-1} (mean value 40.2 ± 38.3 m^{-1}). Spectral slopes (S) varied from 0.011 to 0.018 nm^{-1} (average 0.015 ± 0.001 nm^{-1}). Specific absorptivity (a_{320} normalized per unit DOC)

presents a wide range of values from 0.9 to 7.0 L m^{-1} mg DOC^{-1} (mean value 3.9 ± 1.5 L m^{-1} mg DOC^{-1}). We observed differences between surface and bottom values of a_{320} and specific absorptivity in all ponds where this was measured (**Table 6**). All S values derived from spectra did not vary significantly between the two depths. More observations are needed to determine accurately if differences between surface and bottom waters are significant.

For the 2005 summer season (data not available in 2004), surface water of ponds showed a maximum of fluorescence (in emission spectra for excitation at 370 nm) in the range 448-468 nm (only one value <458 nm: KUJ4), which is slightly above wavelengths indicative of a terrestrial origin for DOM (**McKnight et al. 2001**) (**Figure 6**). Wavelengths of maximum fluorescence were not significantly different in surface and bottom waters (**Wilcoxon, P = 0.125**). The fluorescence index (FI) at the surface of thermokarst ponds varied from 1.12 to 1.36 (mean value 1.22; median value 1.21 ± 0.06). The FI values in bottom waters varied from 1.19 to 1.96 and were significantly higher than at the surface (**Paired t-test; P = 0.016; Table 6**). The values obtained in our study are below the range published by **McKnight et al. (2001)**, but are mainly situated within the range of values reported in the literature for reference fulvic acids. The Suwannee River fulvic acids, a terrestrial reference fulvic acid of the International Humic Substance Society (IHSS), present values from 1.15 to 1.40 (e.g. **Schwede-Thomas et al. 2005**). For the microbial reference fulvic acids was obtained from Lake Fryxell in the McMurdo Dry Valleys of Antarctica, with values ranging from 1.56 to 1.90 (**McKnight et al. 2001; Fulton et al. 2004; Schwede-Thomas et al. 2005**). These differences can be attributed to difference between the unique optical design and light source of each instrument (**Cory and McKnight, personal communication**). **Schwede-Thomas et al. (2005)** observed values that were consistently lower for the Cary Eclipse, which is consistent with our observations. In this latter study, the difference between the indices was up to 0.26 units lower with the Cary Eclipse compared with the Hitachi spectrofluorometer. Even considering this possible instrumental effect, the majority of thermokarst appears to have DOM mainly derived from terrestrial origin. A difference of 0.1 in FI may be indicative of a difference source of fulvic acids (**McKnight et al. 2001**). Differences were observed between surface and bottom waters in a channel of the BYL site. The contribution of the microbial community to the pool of DOM is clearly indicated in its bottom waters. However, with two data points, it is difficult to draw conclusions.

Fluorescence intensities in synchronous fluorescence spectra were higher at the shorter wavelengths (< 410 nm) for the majority of thermokarst ponds (**Figure 7**). All ponds featured principal peaks (**emission wavelengths: 300(I), 362(II), 395(III), 416(IV), 439(V), 487(VI), 514(VII), 560-575(VIII) nm**) often accompanied with small shoulders at shorter and longer wavelengths. Fluorescence spectra with a more significant and apparent shoulder around peak **VI** and **VII** were observed at the Boniface site (forest tundra, ponds originating from a palsa) and in ponds where peat was present (ponds in periphery of palsas or ponds with peat in their surroundings): KUJ1, BGR3, BGR8 (**Figure 7 a., b.** and **c.**). All spectra were relatively similar in shape but differed in the intensity of each peak. Differences were observed between surface and bottom water fluorescence spectra (**Figure 8**). The intensity of fluorescence was generally higher at the surface (BGR1, BGR5 and KWK1), whereas the opposite was found in KWK2. In addition, in surface water from BGR1 a peak appeared at longer wavelengths that did not exist in the bottom waters. However, this peak appeared only in this sample and was not observed in other ponds. The fluorescence ratio HI-1 (400/360 nm) varied from 0.35 to 1.44 (mean value of 0.67 ± 0.24) while HI-2 (470/360 nm) varied from 0.72 to 1.24 (mean value of 0.92 ± 0.13). These two humification indices are well correlated (**r = 0.909, n = 78**). We observed slightly higher values in bottom waters (except in BGR1 where the opposite trend was observed) but the differences were not significant (**paired t-test, P >0.05; Table 6**).

Dissolved gases

We often observed bubbles at the surface of the water and could smell methane walking along the margins of ponds, indicating the escape of gases and the existence of anoxic conditions in these aquatic systems. The ponds were in most cases oversaturated in CO_2 and CH_4 and presented a wide range of concentrations (86-10380 ppmv CO_2, mean value 1846 ± 2131 ppmv CO_2; 0.9 – 64 ppmv CH_4, mean value 20 ± 15 ppmv CH_4; **Table 7**). The concentration of CH_4 was not correlated with the concentration of CO_2. Accordingly, ratio of CH_4/CO_2 varied considerably in surface waters. We found weak but significant positive correlations between CO_2 and DOM characteristics (**Figure 9**). Such correlations were not found between CH_4 and DOM.

We observed great differences between surface and bottom waters (**Table 6**). CO_2 was approximately 5 to almost 10 times higher in bottom waters as compared to the surface. CH_4 showed an even more important increase with depth, with concentrations from 2 to 125 times higher in bottom waters. If we assumed atmospheric values being 379 ppmv of CO_2 and 1.77 ppmv of CH_4 (**IPCC 2007**), all sampled ponds were oversaturated in CH_4 and almost all of them in CO_2 (except BGR1, BYL1, BYL16, BYL4, the last 3 being shallow ponds on depressed polygons). In bottom waters, the saturation compared to atmosphere concentration was even more important (**Table 6**). **Figure 10** shows results for consecutive sampling in 3 ponds during the summer 2005. In BYL2, there is clearly an increase in the concentrations of both gases from afternoon to the night time, followed by a rapid decrease in early morning. This pattern is less evident in BYL4, although similar, and it is subject to a large standard deviation. BGR5, the subarctic pond, showed a slight decrease during night time, followed by a net increase in the early morning until noon. It seems that a decrease followed this increase in the afternoon.

Biological components

The planktonic Chl *a* concentration ranged from 0.3 to 8.8 μg L^{-1} (mean value of 2.6 ± 2.1 μg L^{-1}) except in one case where it reached 54 μg L^{-1} (AAQ3). We observed a high biomass of unidentified filamentous and mat-forming algae in some ponds, indicative of a relatively productive ecosystem.

Bacterial abundance varied greatly among ponds and sites (range of 0.7 to 16.8 $\times 10^6$ cells mL^{-1}; **Table 7**). We found a relationship between the bacterial abundance and ammonia (NH_4) (**Figure 11 a. ; $r^2 = 0.62$; n = 27; $P < 0.0001$**), and a weaker but significant relationship with total phosphorus (**Figure 11 b. ; $r^2 = 0.20$; n = 28; P = 0.0143**). Samples available for bottom waters generally showed higher bacterial abundance than in surface waters (except BGR5).

Bacterial production, estimated by the leucine incorporation rates, varied from 103 to 1195 pmol leu L^{-1} h^{-1} in surface water (mean = 476 ± 76; n = 13; **Table 8**) and from 167 to 1260 pmol leu L^{-1} h^{-1} in bottom waters (mean = 757 ± 503 pmol leu L^{-1} h^{-1}; n = 4). The bacterial production at the two depths was not significantly different (**t-test; P = 0.080**). Results from size fractionation by prefiltration through 3 μm polycarbonate membranes

showed that 82% (BGR1-surface), 99% (BGR1-bottom), 56% (BGR5-surface) and 100% (BGR5-bottom) of leucine incorporation was associated with suspended particles > 3 μm.

Nutrient limitation experiments were performed in two ponds (BGR1 and BGR5). Differences between treatments were significant in both ponds (**one-way ANOVA, P <0.001). Holm-Sidak** posthoc comparisons showed that the treatment with the addition of both glucose and PO_4 was significantly different from control in both ponds (**P < 0.05**), whereas the treatment with glucose only was significantly different from control in BGR5 (**P < 0.05**) (**Figure 12**). This result indicates that the bacteria are limited in glucose and/or phosphate.

Discussion

As high latitude aquatic ecosystems are situated in a landscape with slow chemical weathering and minimal anthropogenic influences, they typically produce ultra-oligotrophic freshwater system due to low inputs of nutrients and organic carbon from terrestrial surroundings (**Pienitz et al. 1997a and b**). Thermokarst ponds are clearly contrast with these systems. The ecosystems studied here encompassed a broad range of habitats, from subarctic tundra to arctic tundra. The data gathered from our study of 57 ponds revealed heterogeneous conditions within and among sites, with relatively high nutrient concentrations and heterotrophic productivity.

Physical and geographic-environmental variables

All ponds sampled typically present shallow water and small surface areas (**Table 5**). Despite these similar characteristics, ponds varied considerably in many limnological properties, even on a small geographic scale (within a given site). Moreover, even though ponds were shallow, we observed significant differences between surface and bottom waters (**Table 6**). The ponds originating from mineral permafrost mounds (i.e. BGR and KWK sites; **Figure 1 a.** and **c.**) were consistently deeper and more turbid than those originating from sites where a peat cover was present.

Temperature profiles, when available, revealed a stable thermal stratification established in many ponds of the discontinuous permafrost area, particularly the ones originating from lithalsas. In the other ponds, thermal stratification did not develop, likely because of

their shallow depth, but nevertheless the conditions were not isothermal (**Figure 3**). The long-term monitoring of temperature in BGR1 yielded information about the thermal structure of these systems over an entire year (**Figure 4**). The pond had an ice cover from approximately the end of November to the end of April, with two periods of mixing at the beginning of summer and in early autumn (**Figure 4 c.**). Hence, the pond is apparently dimictic. However, a close examination to the summer 2005 data showed some vertical mixing at the end of July (**Figure 4 b.**). It appears that there was some diurnal stratification at the end of July 2005. At first glance, the pond seems dimictic but the presence of other short period of mixing encourages us to infer that it is more polymictic. These short periods of mixing are probably associated with intense period of strong wind and cooling of temperature. The other ponds with similar depth from this site and from other sites in discontinuous permafrost area presumably showed the same pattern.

One of the most striking characteristics of the thermokarst ponds was the remarkable pattern of colors and turbidity, particularly in BGR and KWK sites (**Figure 1 a.** and **c.**). It is well known that near-surface heating of somewhat colored and/or turbid lakes of moderate size helps to establish an early temperature gradient that prohibits deep mixing (**Kalff 2002**). The analysis of DOC and TSS confirmed the high content of chromophoric DOM (CDOM) and inorganic particles. At the BGR site, a large part of the soil is composed of clays and silts (**Calmels et Allard 2004;** soil composition from 2 to 6.6 m: silt = 21-27%; clay = 78-72%; organic matter = 1.25-1.12%) and the study by **Tietjen et al. (2005)** highlighted the importance of clay minerals as a transport mechanism for soil organic matter transfer from the drainage basin to an aquatic system. They showed that this organic matter adsorbed to clay particles is available to bacteria through desorption. Their experiments showed that a suspension of clay adsorbed preferentially the chromophoric portion of DOC and enhanced photochemical decomposition of CDOM and DOC. In addition, they observed that significant amounts of DOM were desorbed from the clay-organic aggregates into water of low ionic strength and low concentrations of DOM. Solar radiation decomposed the adsorbed CDOM to low molecular organic products and to CO_2 (these issues are discussed more extensively in Chapter 3). The interactions between DOM and clay particles are likely numerous. Adsorption of organic matter onto clay minerals is dependant upon both the type of minerals and the source of DOC (**Tietjen et al. 2005**). It undoubtedly affects the limnological properties of thermokarst ponds. Many interactions, together with the melting of permafrost, are taking

place through time and likely generate these complex optical states, with multiple consequences on the biota. More studies of these interactions in thermokarst ponds are clearly needed.

In contrast to transparent lakes, where only about half of the incident irradiance (300-3000 nm) is converted into heat in the top 10 cm, turbid or colored lakes, characterized by high vertical extinction coefficients, absorb and convert to heat not only the infrared portion of the solar spectrum (> 700 nm), but also PAR (400-700 nm) within a short distance of the water surface (**Kalff 2002 and references therein**). The lowest value of Kd_{PAR} available for thermokarst ponds is comparable to Lake Tooms (Tasmania), a highly eutrophic and colored lake (**Bowling et al. 1986**). The depth at which PAR is absorbed has important limnological implications. All non-transparent lakes convert virtually all irradiance into heat near the surface. Therefore, such lakes stratify earlier in spring and have colder hypolimnia than transparent lakes of similar size, wind exposure and climatic zone. A longer period of stratification increases the possibility of hypolimnetic hypoxia (**Kalff 2002**). This is precisely what we observed in many thermokarst ponds, which presented a net decrease of oxygen with depth.

The range of nutrient concentrations in thermokarst ponds is wide. Differences in nutrient content can be explained by the drainage basin characteristics, extent of rock weathering and input of allochthonous material, for example from the catchment vegetation. The drainage basins of subarctic thermokarst ponds are typically really small (because of small scale topography and thermokarst soil impermeability), but nevertheless differences (up to 2.5 times for TP) were observed in ponds of close geographic proximity (<200 m). **Howard-Williams et al. (1990)** suggested that the age and stability of a pond may influence its nutrient characteristics: in older, stable ponds there can be a long-term accumulation of nutrients and biomass. Time seems to be an important factor to understand the nature of thermokarst ponds. Despite this variability in concentrations, overall, thermokarst ponds presented relatively elevated nutrients. This observation contrasts with subarctic and arctic lakes, where TP concentrations are usually low (**Lim et al. 2001:** mean 12.7 $\mu g\ L^{-1}$; **Pienitz et al. 1997:** mean 15.5 $\mu g\ L^{-1}$). It may be partly explained by the input of fresh nutrients and carbon from melting permafrost. However, we do not know the importance of this input. On the other hand, in highly turbid ponds, a

fraction of the phosphorus could derive from the inorganic particles themselves. The correlation found between TP and TSS supports this hypothesis.

On the basis of the general relationships between lake productivity and average concentrations of epilimnetic TP established by **Vollenweider (1976),** we estimate that our studied thermokarst ponds fall within oligomestrophic (3 %), mesoeutrophic (33.3%), eupolytrophic (60%), and polytrophic (3%) trophic ranges (n = 30).

DOM characterization

A wide range of DOM concentrations and optical properties (absorption and fluorescence) were found in the thermokarst ponds. Differences in watershed and edaphic characteristics were probably reflected in DOM. The presence of dense vegetation or peat in the watershed likely explains the high DOC content found in some ponds. On the other hand, as discussed above, clays can adsorb organic matter such as humic substances (**Tietjen et al. 2005 and references therein**) in ponds with high inorganic turbidity. Therefore, the sedimentation of these particles may cause a loss of DOM from surface waters through time. Moreover, when the water is filtered to characterize DOM, an unknown fraction of DOM adsorbed to particles can be lost. It is well known that the chromophoric fraction of this adsorbed organic matter (CDOM) can affect the transmission of light in the water column (**Morris et al. 1995, Gibson et al. 2000**) or it can be available to attached bacteria. This phenomenon should be considered carefully in future studies of carbon turnover in thermokarst ponds.

Two neighbouring ponds sometimes showed large differences in DOC, CDOM (a_{320}) or specific absorptivity. For example, BGR1 and BGR2, which are located less than 25 m from each other, presented marked differences: DOM absorbs more than 2 times more light than in BGR2. There are a lot of examples of such discrepancies, which can have great impact on vertical stratification, for example. KWK4 showed a strangely high value of CDOM a_{320} and absorptivity. This value is presented in **Table 3**. More investigations are clearly needed. However, even neighbouring ponds do not necessarily form at the same time. The large differences between DOM characteristics in the two ponds could be associated with their age and associated geochemistry or autochtonous influences. Again, time seems to be an important factor regulating the composition of DOM in ponds. Accurate aging might be a challenging issue for further investigations on thermokarst

ponds. The relatively low slope (S) values found in all ponds of this study indicated typical terrestrially-derived DOM in thermokarst ponds since it is generally accepted that the slope of DOM absorption (S value in the UV-visible region) of microbially-derived or highly degraded DOM is more elevated than for terrestrially-derived DOM or less diagenetically altered material (see reviews by **Markager and Vincent 2000, Twardowsky et al. 2004**). Results obtained with emission spectra encourage this hypothesis of mainly terrestrial origin (**Figure 6; Table 3**). DOM likely originates from soil and plant leaching in the surroundings, erosion of permafrost where organic matter stocked for hundreds of years, and some import via precipitation. As the drainage basin of thermokarst pond is small and the mean annual precipitation is low (414 mm; **Environnment Canada 2000**), storm events could have great impact on the DOM signature and water import in the pond on short time scale. A more detailed study of water budget in thermokarst ponds should be addressed in the future.

Fluorescence spectroscopy in the synchronous-scan mode allows better peak resolution than with conventional fluorescence emission spectra, providing distinct spectral signatures and the possibility to identify the structures responsible for DOM fluorescence (**Senesi 1990**). Our results show that all thermokarst ponds present similar synchronous spectra with 8 main components or group of components (**Figure 7**), suggesting that all the samples contain variable combinations of similar types of fluorophores. Thermokarst ponds seem to present the two types of fluorescence (protein and humic-like), categorized into three principal fluorophore groups which could be responsible for natural fluorescence by **Mopper and Schultz (1993)**. One of these groups emits fluorescence at short wavelengths (λ_{ex} < 280 nm and λ_{em} < 340 nm) and might be composed of protein-like components. The two others, with λ_{em} ranging from 380 to 480 nm (λ_{ex} from 260 to 350 nm) seem to be related to humic substances (HS, **Sierra et al. 2000**). Thus, the major peak before 300 nm (peak I; **Figure 7**) can be associated with dissolved proteins composed of amino acids like tryptophan or tyrosine, or amino acids and proteins whose occurrence is related to recently produced organic matter (e.g. **Coble et al. 1990**; **Sierra et al. 1994**, **Ferrari and Mingazzini 1995**; **Coble 1996**; **Sierra et al. 2000**). Although S and FI indicate a predominance of terrestrial source for DOM, it seems obvious that the autochtonous input is not negligible, as shown by the presence of this peak I (often one of the most important in intensity in many ponds). The other peaks found in our samples are likely associated with humic substances, principally FA (45-65 % in surface waters and

80-90 % in wetlands; McKnight 2003). Note the difference between ponds which that originated from a palsa melting or have peat in their surroundings (**Figure 7 a.** KUJ1, **b.** BGR3 and BGR8, **c.** all BON ponds). All these ponds present a relative higher fluorescence at the longer wavelengths compared to other ponds. We can then associate a contribution from peat to the compounds that fluoresce at longer wavelengths, at least in the subarctic area. In addition, we observe that the HI-2 values of these ponds are significantly higher than for the other ponds and the overall spectra is less define than the others. This situation is maybe explained by a higher complexity of the assemblage of molecules resulting in smoother spectra (**Figure 7 c.**) compared to the highly defined peaks found in some spectra (for example peak IV in KUUJJ3, **Figure 7 a.**). This complexity is also likely related to the presence of complex molecules originating from peat.

Six of our peaks had similar positions in the spectra to peaks found in lake, river and reservoir water samples originating from Finland (**Peuravuori et al. 2002**): I, II, IV, VI, and VII. There was slight difference in peak position (2-7 nm), but this can probably be attributed to the difference in instruments (up to 10 nm according to **Kalbitz and Geyer, 2001**) and settings used in this latter study ($\Delta\lambda$ = 18 nm). We can then expect similar components in our samples. As discussed earlier, the first peak (I) likely mainly associated with the presence of dissolved proteins, as suggested by many other authors (e.g. **Coble et al., 1990; Ferrari and Mingazzini, 1995**; **Lu et al. 2003**). The others peaks were associated by **Peuravuori et al. (2002)** with II: polycyclic aromatics with three to four fused benzene rings; IV: polycyclic aromatics with approximately five fused benzene rings; VI: polycyclic aromatics consisting of about seven fused benzene rings, the most common lignin descriptors. Peak VII has been previously associated with the presence of linearly-condensed aromatic-ring systems bearing electron-withdrawing substituents such as carbonyl and carboxyl groups and/or to other unsaturated bond systems capable of a high degree of conjugation as well as to the presence of high molecular weight fractions of humic substances (**Senesi et al. 1994 and reference therein**). We did not find any specific information about our peaks III and VIII in literature. However, we can also classify these peaks in relation to source, weigh and age as in **Retamal et al. (2006)**. Then, peak I falls in the low molecular weight (LMW) category of young autochtonous DOM, peaks II to IV in medium MW (MMW) more complex and older components, mostly fulvic acids originating from allocthonous

processes, and peaks V to VIII fall in the high MW (HMW), mostly composed of humic acids. The abundant microbes and possibly unique assemblages, as compared to the more studied aquatic systems (marine and temperate lakes), may have contribute to transform DOM and generate distinctive peaks in the SF spectra of thermokarst ponds. It should not be forgotten that the only adjustment between samples was for temperature (room temperature). However, it is well known that many factors can affect fluorescence spectra (**Senesi 1990**).). Many studies explore these different effects on fluorescence (Concentration of DOM: **Miano and Senesi 1992, Mobed et al. 1996, Westerhoff et al. 2001**; Chl a: **Wiley and Atkinson 1982**; Ionic strength: **Ghosh and Schnitzer 1980, Mobed et al. 1996**; Temperature: **Dujmov et al. 1992**; Interactions with metal ions: **Cabaniss and Schuman 1987**; pH: **Laane 1982; Wiley and Atkinson 1982; Cabaniss and Schuman 1987; Mobed et al. 1996; Pullin and Cabaniss 1995; Westerhoff et al. 2001**). To summarize, humic substance concentrations in the range of 5-100 mg/L had little effect (**Mobed et al. 1996**), ferric iron and copper affect fluorescence intensity (**Cabaniss and Schuman 1987**), increases of temperature increase efficiency of non-radiative deactivation (**Dujmov et al. 1992**), intensity decreases with increasing ionic strength (**Ghosh and Schnitzer 1980**) and pH affects intensity and spectral shape (**Cabaniss and Shuman 1987**). We do not know the importance of many of these factors in our samples, but we do know their pH. The differences in intensity of fluorescence spectra between ponds could be in part due to these differences in pH (**Pullin and Cabaniss 1995, Mobed et al. 1996**). After all, pH ranged from 5.1 to 9.2, a very wide range. In general, the overall fluorescence intensity decreases as pH increases (**Miano and Senesi 1992**).

Differences were observed between surface and bottom water but they represent essentially a difference in intensity of the spectra. All ponds except KWK2 showed a lower intensity of fluorescence and a higher index of humification (HI-2; **Table 6**) in bottom water. It seems that the complexity and degree of humification of compounds in the bottom waters are higher, where the light is highly decreased by CDOM and inorganic turbidity. The contrast of KWK2 is perhaps explained by a different microbial community exploiting a different amalgam of molecules. In addition, an uncommon large peak (VIII) appeared around 575 (VIII) nm in BGR1 surface water. This is the only spectrum in which we observed this peak. Although this peak has been previously observed in our other ponds (but with really small intensities), we are unable to explain

its high intensity here. It is likely a storage artefact. These differences between surface and bottom waters indicate clearly that DOM showed a spatial variability within ponds.

Dissolved gases

In our study, almost all ponds were oversaturated in CO_2 and CH_4 (using global atmospheric concentrations of 379 ppmv in CO_2 and 1.77 ppmv in CH_4; (**IPCC 2007**). The only exceptions were found in depressed polygons (BYL sites) where ponds were slightly undersaturated. It is important to keep in mind that dissolved CH_4 is likely a small fraction of the methane produced in the ponds (**Walter et al. 2006**) since methane is about 27 times less soluble in water than in the air.

We observed weak but significant correlations between dissolved CO_2 and many descriptors of DOM quantity and quality (**Figure 9**). Nowadays, remote sensing tools are available to describe DOM at long range. Accordingly, we can hypothesize that DOM characterization could eventually be used as a tool to estimate the importance of dissolved CO_2 concentrations in water. All observed correlations were positive. Therefore, quantitatively, an increase in dissolved organic carbon (DOC) concentration led to an increase of dissolved CO_2 in water, which is intuitive. The more DOM that is available, the more it can be consumed and respired by bacteria or photobleached. In earlier studies, CO_2 oversaturation in lake surface water was often correlated to the concentration of DOC (**Hope et al. 1996, Riera et al. 1999, Sobek et al. 2003**). Absorptivity and HI-1 are qualitative indices of DOM; an increase of these indices indicates the enhancement of humification of DOM. According to **Sobek et al. (2003)**, the major source of CO_2 oversaturation in boreal lakes is most likely the mineralization of imported organic matter. We suggest that the allochtonous terrestrially-derived and complex organic matter with a high degree of humification in thermokarst ponds is the major source of C causing oversaturation in surface waters. From a qualitative point of view, the more complex is the DOM in a pond, the more CO_2 is found in its waters. For example, this is clearly shown in **Table 7** where one can observe the highest CO_2 concentrations in ponds from the KUJ and BON sites, ponds that all have SF spectra with a higher relative intensity in the HMW category (peat is present; **Figure 15**). Direct bacterial utilization and photochemical mineralization, as well as photochemically facilitated bacterial metabolism, contribute to the mineralization of allochtonous DOC

into CO_2 (**Sobek et al. 2003 and ref therein**). We suggest that a great part of this CO_2 is produced by photolysis of complex molecules found in the surface waters of thermokarst ponds. Another fraction is likely due to respiration of organisms, but no correlation was been with bacterial abundance or productivity. However, both gases were more concentrated in bottom waters, indicating a benthic source mainly, wheras CH_4 is the product of anaerobic processes. Hence, higher correlations with organic carbon might eventually be found in hypoxic bottom waters, but we do not have enough data from bottom waters to verify these relationships. It is possible that dissolved organic matter also has indirect effects on microbial respiration through its control on thermal and light regimes.

Diel changes in dissolved CH_4 and CO_2 were observed in BGR5 and BYL2 (**Figure 10**), similar to the variations observed by **Hamilton et al. (1994)**, with a slight decrease during the afternoon and increase in the morning. BYL2 is less exposed to wind mixing and sunlight than are the ponds situated on depressed polygons, maybe partly explaining the high concentrations of both gases. Changes in gas concentrations occurred almost synchronously in the 3 ponds. However, BYL4 (depressed polygon pond) presented an opposite trend in CH_4 concentrations compared to the other ponds. In addition to the influence of physical factors on gas concentrations, thermokarst ponds shelter a complex and diverse consortium of microbes undoubtedly affecting gas fluxes. In the arctic ponds, methane concentration was always at least 3 times higher than the atmospheric reference concentration of 1.7 ppmv. However, carbon dioxide fell under the atmospheric concentration (BYL4 always undersaturated and BGR1 only in the afternoon). In the subarctic ponds, the CO_2 concentration was 2 to 14 times greater than the atmospheric values. In the work of **Hamilton et al. (1994)**, a pond with a mineral bottom (compared to pond with an organic bottom, principally composed of peat) consistently showed the lowest values of both gases.

We also observed differences in the concentrations of gases between surface and bottom waters (data only sampled in the deeper stratified ponds). CO_2 was 4 to almost 10 times higher and CH_4 from 2 to almost 125 times higher at the bottom of ponds. These bottom waters were always hypoxic and often presented higher bacterial abundances than at the surface. Methane production occurs only by anaerobic processes in strictly anoxic environments, such as in wetlands and ponds (**Reeburgh et al. 1998**). The high

concentration of gases in bottom waters is undoubtedly linked to high respiration rates from aerobic and anaerobic bacterial communities, specifically from benthic communities. However, it is well known that thermal stratification and the formation of a thermocline impose some restrictions on nutrient and gas circulation (CO_2: **Urabe et al. 2005)** toward the upper layers (**Kalff 2002**). Accumulated hypolimnetic gases would then transfer into surface waters when the thermal stratification weaked or disappeared. The autumn may be a time of elevated pCO_2 in surface waters (**Cole et al. 1994**). The spring also may likely lead to increased fluxes when the ice breaks up and releases the accumulated gases respired during the winter, dissolved gases and bubbles of methane. However, it is particularly challenging to measure winter and spring fluxes in these remote regions. In this context, it should not be forgotten that methane is released as bubbles (bubbling or ebullition; **Walter et al. 2006**) as a dominant pathway (95% in **Walter et al. 2006**), and passes easily through the thermal barrier.

Gas fluxes can be calculated from dissolved concentrations (e.g. **Matthews et al. 2003**) but this calculation requires wind speed, which was not measured in our study. However, the flux is proportional to the difference in concentration between the bottom of the boundary layer (water) and the top of the boundary layer (atmosphere). High concentrations of both gases in most of the ponds that we sampled support the hypothesis that thermokarst ponds represent a source of carbon to the atmosphere (except for depressed polygons, where the concentration of CO_2 was similar to the atmospheric value). This agrees with results obtained from Alaskan lakes and rivers that were considered as efficient gas conduits to the atmosphere (**Kling et al. 1991**). **Hamilton et al. (1994)** studied gas fluxes in ponds and surrounding vegetated surfaces in the Hudson Bay lowlands in Canada and estimated that even though ponds cover only 8-12% of the Hudson Bay lowlands area, they accounted for 30% of its total CH_4 flux to the atmosphere. In their study, the ponds were constant net sources of CH_4 and CO_2 to the atmosphere at mean rates of 110-180 mg CH_4 m^{-2} d^{-1} and 3700-11 000 mg CO_2 m^{-2} d^{-1}.

Direct and intensive measurements are needed to know how widespread these losses from surface waters are, and thus to what extent high latitude carbon budgets will be affected by climate changes. A review by **Batlett and Hariss (1993)** showed that boreal and tundra wetlands could account for between 0.03-0.04 Tg CH_4 y^{-1} (or Gt CH_4 y^{-1}). pondThis is not negligible compared to the anthropogenic land use change (1.6 GtC y^{-1} or

TgC y^{-1}) or emission from fossils fuels in the period 2000-2005 (7.2 GtC y^{-1} or TgC y^{-1}) (**IPCC, 2007**).

Zimov et al. (1997) highlighted that landscape disturbances caused by the melting of permafrost and the creation of thermokarst ponds can lead to high CH_4 emissions. CH_4 presently accounts for 15% of current radiative forcing on climate (**Moore et al. 1998**). We can hypothesize that climate change could lead to a local increase in gas emissions with an increase of thermokarst pond formation. In some regions, however, thawing of permafrost could lead to the complete draining of the soil **(Smith et al. 2005). Gorham (1991)** has suggested that an effect of climate warming will be drying of peatlands, leading to less CH_4 flux to the atmosphere. However, this might rather be a long-term response and will depend on the type of soil and the precipitation regime. On the other hand, as we have seen, adjacent to our study sites, ponds can fill up with vegetation (**Figure 13**) and carbon fluxes could potentially reverse after a while. We measured the gas concentration from pond that was a recolonized by plant and was in in an intermediate state, but it was still oversaturated in both gases (KWK2-B; **Table 2**). Long-term monitoring would be needed to understand each step of thermokarst pond formation and the consequences for global carbon balance. Thermokarst processes and associated changes in the area occupied by water should be taken into account in future gas-exchange studies of northern ecosystems.

Biological components

Planktonic Chl *a* concentrations found in arctic ponds (BYL site) were in the range of concentrations found in previous studies (**Vézina and Vincent 1997**). Although the trophic status estimated from TP concentrations in the thermokarst ponds ranged from oligomesotrophic to polytrophic, the concentration of Chl *a* was relatively low. Usually, low biomass and productivity are a result of nutrient limitation **(Kalff 1971**; **Alexander et al. 1980**) and grazing by zooplankton, which often form the top of the food chain in these systems (**Hansson et al. 1993**; **Rautio 2001**; **Rautio and Vincent 2006**). Nutrients were apparently not limiting in thermokarst ponds. In addition, there was no significant relationship between Chl *a* and TP, which is in striking contrast to previous investigations. Therefore, we can postulate that zooplankton grazing is having a large impact on phytoplankton abundance in thermokarst ponds. High zooplankton biomass was indeed observed in all arctic ponds. In subarctic ponds, zooplankton was clearly

more abundant than in rock ponds and many temperate lakes (**J. Turgeon pers. comm.**). In addition, high turbidity and CDOM concentration certainly impact the PAR available to photosynthetic organisms.

Within aquatic ecosystems, pelagic bacteria constitute an important food source to protists and metazoans (**Cho and Azam 1988**). The abundance of bacteria was quite high in thermokarst ponds and comparable to concentrations found in mesotrophic to eutrophic lakes (**see the review by Wetzel 2001**). Moreover, the abundance determined by epifluorescence microscopy is possibly underestimated since many bacteria were near the nominal size of the filter pores (**Gasol and Moran, 1999**). Likewise, particle-attached bacteria cannot be counted properly with this method. They surely accounted for a variable but significant part of the community (see below).

This abundant bacterial community presented a relatively high productivity (476 ± 76 pmol leu L^{-1} h^{-1}; n = 13; production was not measured in arctic ponds) compared to the ocean (0.04-230 pmol leu L^{-1} h^{-1}; **Steward et al. 1996**) or to subarctic large river (132 pmol leu L^{-1} h^{-1}) and estuary (7.5 pmol leu L^{-1} h^{-1}) (**Vallières, 2007**). Thermokarst pond productivity falls within the range of temperate lakes (75-1229 pmol leu L^{-1} h^{-1}, the maximal value being from an eutrophic lake; **Del Giorgio et al. 1997**). The bacterial community might hence play an important role in DOM cycling. In addition, the fractionation of water samples showed us that a significant part of total bacterial productivity (56-100%) was associated with particle-attached bacteria. The importance of particles in heterotrophic productivity was indisputable in the bottom waters (>99.9% attributed to particles-attached bacteria). This is not surprising since particle-associated enzyme activity is frequently found to be much higher than enzymatic activity associated with the free-living microbial community (**Arnosti 2003**). The transformation of organic matter by free-living heterophic bacteria is discussed in **Chapter 3.**

Granéli et al. (2004) previously shown that pelagic bacteria in lakes and ponds of the high Arctic seem to follow the general pattern of phosphorus limitation observed in many temperate and tropical freshwater systems. Our results on two subarctic ponds showed that carbon and phosphorus in BGR1 and carbon in BGR5 were limiting for the growth of heterotrophic bacteria. However, glucose is considered as very labile carbon. BGR5 had higher DOM than BGR1, and synchronous fluorescence spectra indicated that BGR5 also

had a pool of DOM somewhat richer in protein-like components (as indicated by the fluorescence peak I; **Figure 8**). However, as the water was unfiltered, grazers were present in the media. It is possible that grazers were more abundant and further inhibited growth of their preys in BGR1. As we do not know the importance (abundance, diet etc.) of these grazers, it is difficult to draw conclusions. Additionnal nutrient limitation experiments would be undoubtedly needed.

Conclusions and perpsectives

Evidence has accumulated indicating that a majority of the world's lakes are net sources of CO_2 to the atmosphere (**Kling et al. 1991**; **Cole et al. 1994**), and that CO_2 emission rates from lakes are related to their organic carbon content (**Kling et al. 1991**, **1992**; **Hope et al. 1996**; **del Giorgio et al. 1997; Sobek et al. 2003**). The creation of new ponds and subsequent mobilization of carbon could then account for increases in emissions. Thermokarst ponds sampled in the present study follow this pattern of increasing oversaturation at higher organic carbon concentrations. Based on CO_2 oversaturation in lakes worldwide, **Cole et al. (1994)** suggested that lakes can potentially be important conduits of carbon from terrestrial sources to the atmosphere. The yedoma (see Introduction for description) carbon beneath thermokarst lakes in Siberia is decomposed by microbes under anaerobic conditions, producing methane that is released to the atmosphere primarily by bubbling (**Zimov et al. 1997, Walter et al. 2006**). These authors estimated that thaw lakes in North Siberia emit 3.8 teragrams of methane per year, which increases present estimates of methane emissions from northern wetlands by between 10 and 63 percent. Furthermore, the Pleistocene age of the methane emitted from hotspots along thawing lake margins indicates that this positive feedback to climate warming has led to the release of old carbon stocks previously stored in permafrost. In Eastern Canada, higher emissions of CH_4 and CO_2 have been measured over wetland ponds compared to adjacent vegetated surfaces on the Hudson Bay Lowland (**Hamilton et al. 1994**). Any change in the ratio of pond to vegetated area, as may occur in response to climate warming, would affect the total fluxes of this region.

Currently, the carbon content of Earth's atmosphere has increased from ~360 gigatons (Gt) —mainly as CO_2— during the last glacial maximum to ~560 Gt during preindustrial times and ~730 Gt today. The largest such reservoir is the ocean (40,000 Gt, of which

2500 Gt is organic carbon), followed by soils (1500 Gt) and vegetation (650 Gt). There is also a large geological reservoir, from which ~6.5 Gt of carbon are released annually to the atmosphere by burning fossil fuels (**Zimov et al. 2006**). In addition, 90% of Arctic permafrost, which contains large quantities of organic matter, is set to disappear over the next century (**Pearce 2006**). The consequences are discussed and debated. Local permafrost collapse may act as a large local source of carbon to the atmosphere that would offset carbon gains in the remainder of the landscape (**Hobbie et al. 2000**). **Waelbroeck et al. (1997)** proposed that because of partial thawing of permafrost and the subsequent increase in nutrient availability, the tundra's response may be a long-lasting increase in C accumulation following a temporary increase in CO_2 emissions.

Projected climate warming means higher precipitation and higher annual mean temperatures (**IPCC 2007**). This may increase the likelihood of thermokarst initiation on a larger scale. However, depending on soil composition and permafrost degradation, melting of permafrost can either lead to the formation or draining of thermokarst ponds. Permafrost is overlain by the active layer and the depth of this layer is a reflection of the dynamic equilibrium between hydrological and thermal properties of the soil and atmospheric conditions (**Hinzman et al. 1991**). Climate-related changes in this layer will have a wide-ranging influence on the transport of water, solutes and particulate materials. Continuous and discontinuous permafrost will likely be affected differently.

The present study has contributed to increase basic limnological knowledge on thermokarst ponds. They are undoubtedly productive systems and a source of greenhouse gases to the atmosphere. However, our study represents an instantaneous "picture" of their summer limnological properties. Even if they were to represent a source of carbon throughout the year, complete draining or terrestrialization processes could transform this "carbon reactor" into a carbon sink in the long-term. Of great concern is whether or not there are positive feedbacks associated with the formation of thermokarst ponds that may accelerate climate change (**Lawrence and Slater 2005**).

Our results seem to show that the quantity and quality of organic matter (mainly allochtonous, but with an autochtonous contribution too) mobilized in ponds have great impacts on the ability of thermokarst ponds to act as a source of carbon, mainly as CO_2 fluxes. It seems clear that fluxes are higher when organic content is high (high DOC,

thermokarst ponds in peatland mainly) than the inverse (lower DOC, thermokarst in mainly inorganic soil). However, it should not be forgotten that higher productivity of particle-attached bacteria are associated with ponds with high inorganic turbidity, and that stratification keeps important concentrations of captive CO_2 and CH_4 below the thermocline for an important period during the year. If the age of a pond proves to be a crucial element affecting its stability and its nutrients characteristics, (for example through composition and temporal variability of the microbial community or plant colonization) it will undoubtedly affect gas fluxes. Then, the quality of DOM, the temperature and the turbidity will likely influence the temporal variability of gas fluxes because they directly affect the stratification. Many factors are interacting to control regional and large scale variations of carbon fluxes in thermokarst ponds. Finding and understanding all the factors that control these fluxes of carbon in arctic and subarctic aquatic systems is essential for predicting how these regions will respond to global change. On a smaller scale, understanding the dynamics of the DOC pool by studying the interaction of its different transformation processes in some ponds is a prerequisite for modelling the global carbon cycle and will be discussed in the next chapter.

Figure 1: Photographs of different ponds found in our study sites
a. and **b.** Ponds formed on lithalsas at an advanced stage in the discontinuous permafrost area with dense shrubs (Nunavik, a: KWK site N55°19' W77°30'; b: KUJ site N55°13' W77°44'). **c.** Different stages of development of thermokarst ponds over lithalsas in the discontinuous permafrost region (Nunavik, BGR site N56°36' W76°12'). **d.** Pond formed along the margins of a forested palsa (Boniface River site N57°30' W76°14'). **e.** Ponds formed in polygonal ice-wedges (continuous permafrost area, Nunavut, Bylot Island Site N73°09' W79°58').

a.

b.

c.

d.

e.

Figure 2 : Permafrost distribution in Eastern Canada
Our principal study sites are situated near location indicated on the map. **1**: Sirmilik National Park on Bylot Island ponds named **BYL. 2**: Boniface River ponds named **BON. 3:** Umiujaq ponds named **BGR** and **UMI. 4:** Whapmagoostui-Kuujjuarapik ponds named **KUJ, BOU** (sites separated by 100 km of KUJ) and **KWK** (sites separated by 18 kilometres of KUJ) (http://atlas.nrcan.gc.ca).

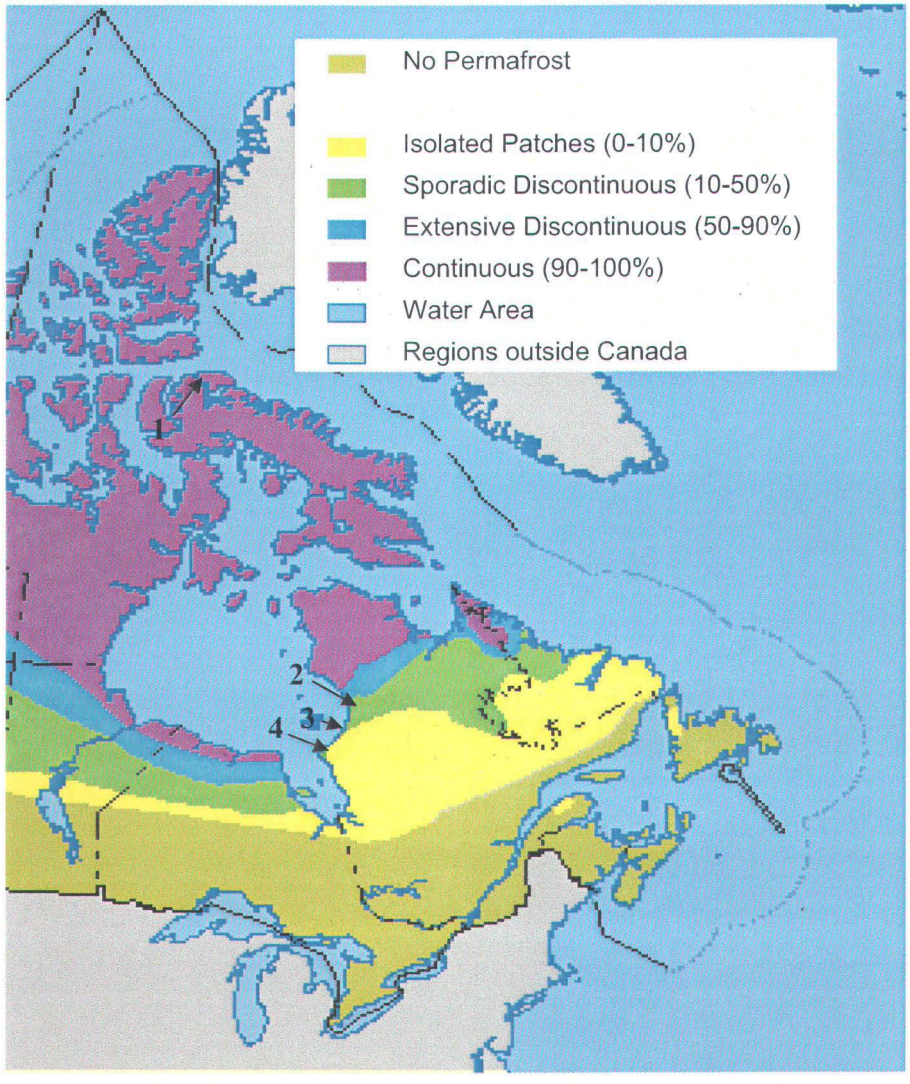


Figure 3: Typical physicochemical profiles of stratified thermokarst ponds showing temperature (solid line) and the percentage of dissolved oxygen (dotted line)
a. BGR4 sampled on July 6th 2004 at 13h45 with the Idronaut probe, b. BGR4 sampled on July 13th 2005 at 15h00 with the YSI probe, c. BGR1 sampled on July 8th 2005 at 14h07 with the YSI probe, d. BGR5 sampled on July 10th at 12h33 with the YSI probe, e. BGR9 sampled on July 9th at 16h38 with the YSI probe and f. BON1 sampled on July 20th at 10h25 with the Idronaut probe.

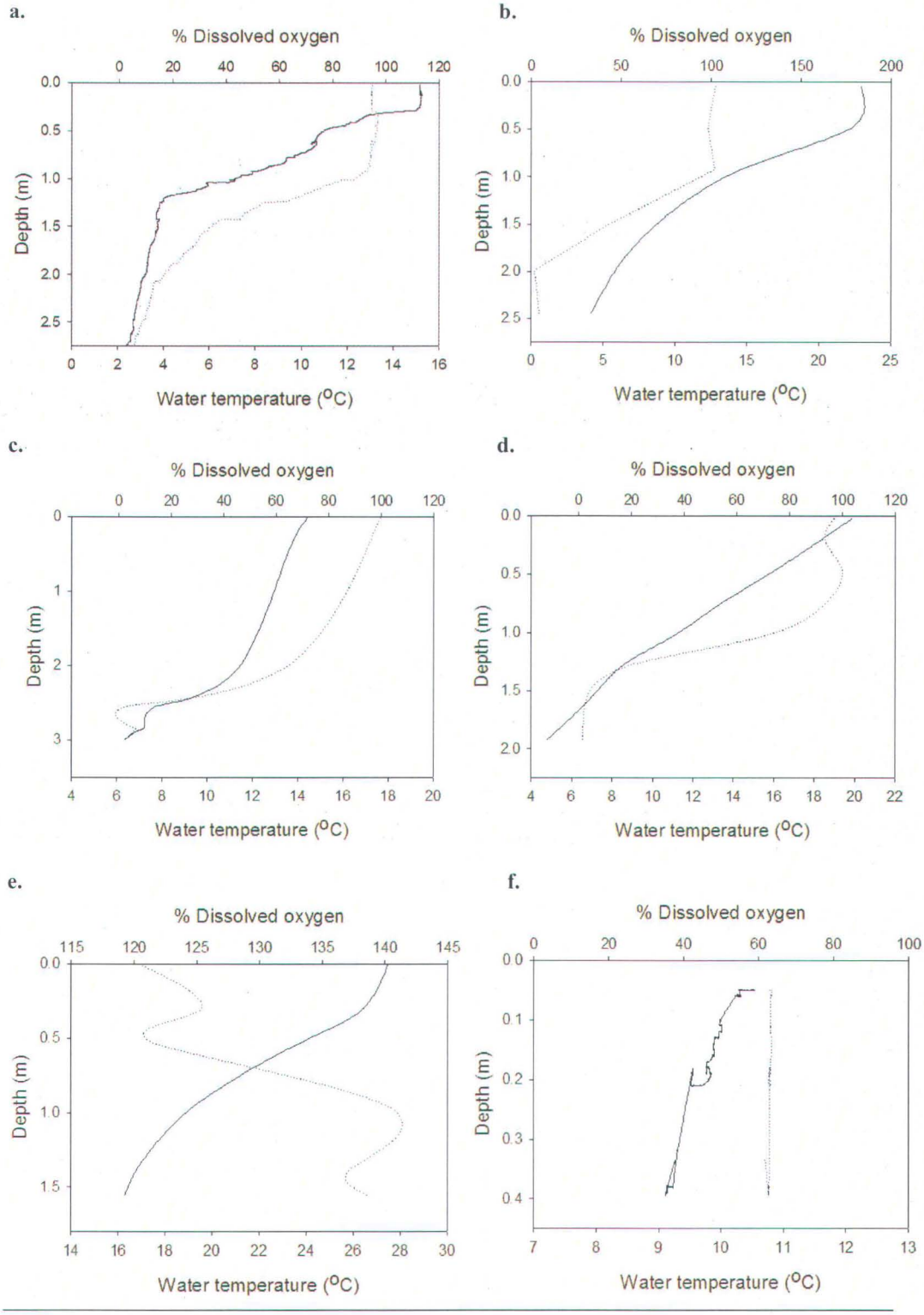
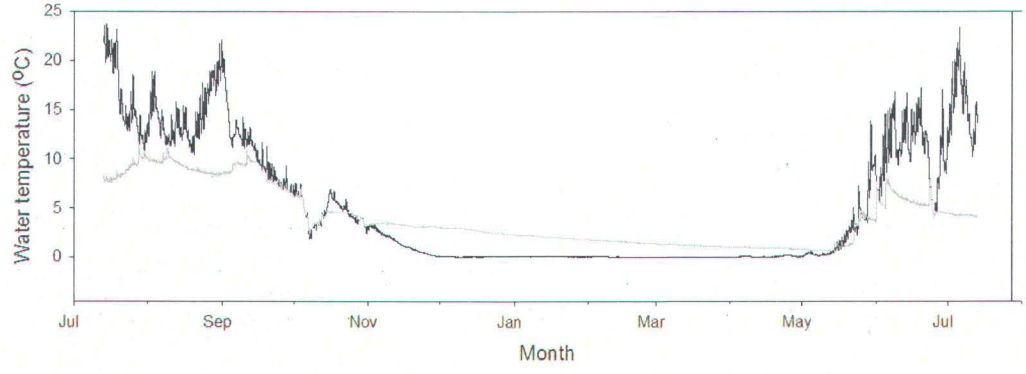


Figure 4: Thermal monitoring of BGR1 from July 2005 to July 2006 at 0.3 m (black lines) and 2.75 m (gray lines).
a. One year monitoring, **b**. Close-up on diurnal stratification in summer, **c**. Close-up on mixing in spring. The pond is approximately 3.2 meters deep.

a.



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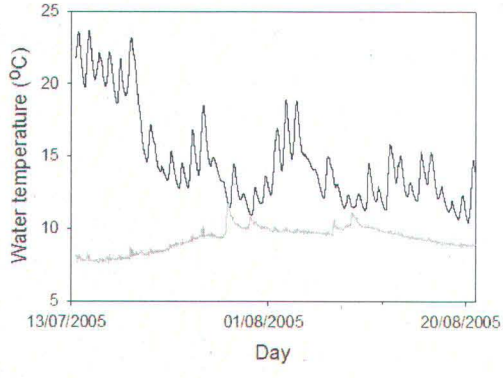

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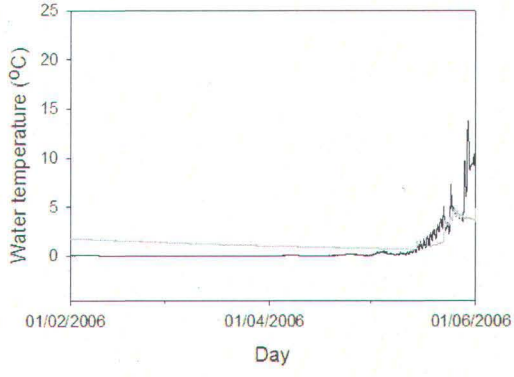


Figure 5: The relationship between total phosphorus and total suspended solids in thermokarst ponds.

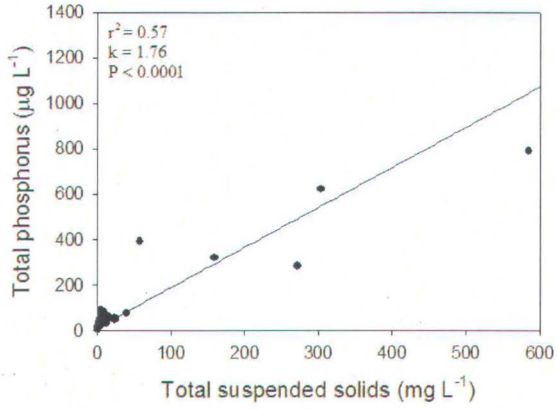
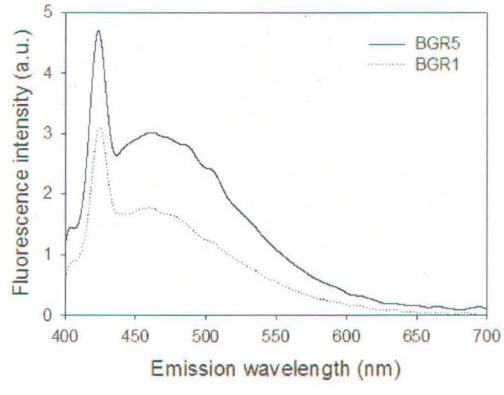


Figure 6: Emission spectra (excitation at 370 nm) of DOM from pond water of the 2005 experiments run at natural pH and DOC concentration. pH and DOC (mg C L^{-1}) are indicated in parenthesis.

a. BGR1 (7.1; 2.5) and BGR5 (6.4; 4.7), **b.** KWK1 (6.9; 9.0), **2** and BYL1(9.2; 9.4). Note that scale vary.

a.



b.

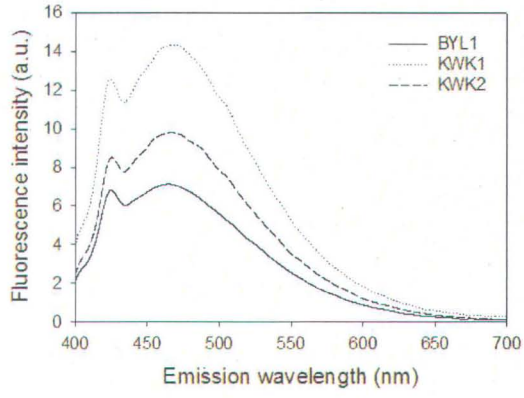


Figure 7 : Overall view of synchronous fluorescence spectra obtained from thermokarst ponds in different regions run at natural pH and DOC concentrations (see Tables 3 and 4)
Ponds sampled near **a.** Whapmagoostui-Kuujjuarapik (insert: KUJ4, a pond sampled in 2004 showing an extremely high fluorescence compared to all other ponds), **b.** Umiujaq, **c.** Boniface River, d. Bylot Island.

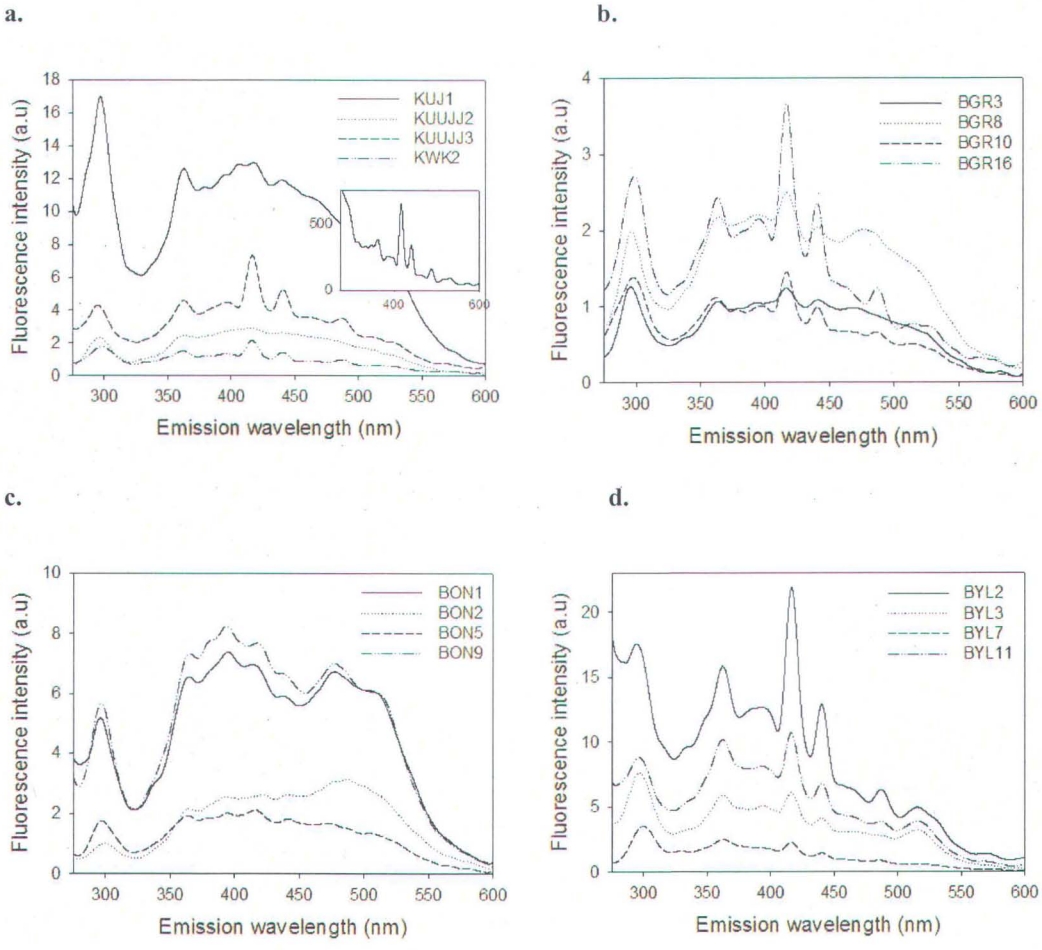


Figure 8: Synchronous fluorescence spectra showing differences between surface (solid lines) and bottom waters (dotted lines) run at natural pH and DOC concentrations (see Table 6)
a. KWK1, **b.** KWK2, **c.** BGR1 and **d.** BGR5

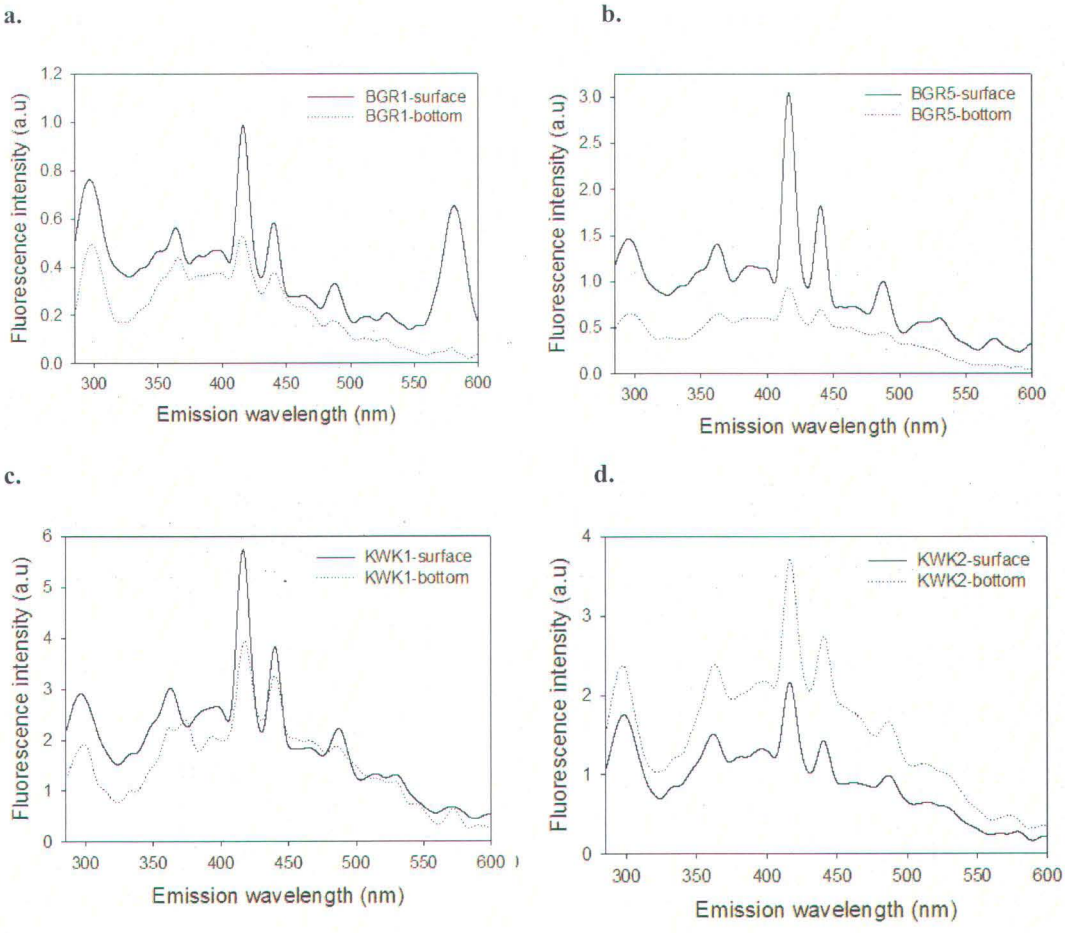


Figure 9: The relationships between the concentration of dissolved carbon dioxide (CO_2) and different DOM characteristics in surface waters of thermokarst ponds
a. dissolved organic carbon (DOC), **b.** absorption of chromophoric DOM at 320 nm, **c.** specific absorptivity of DOC, **d.** humification index calculated from synchronous fluorescence spectra.

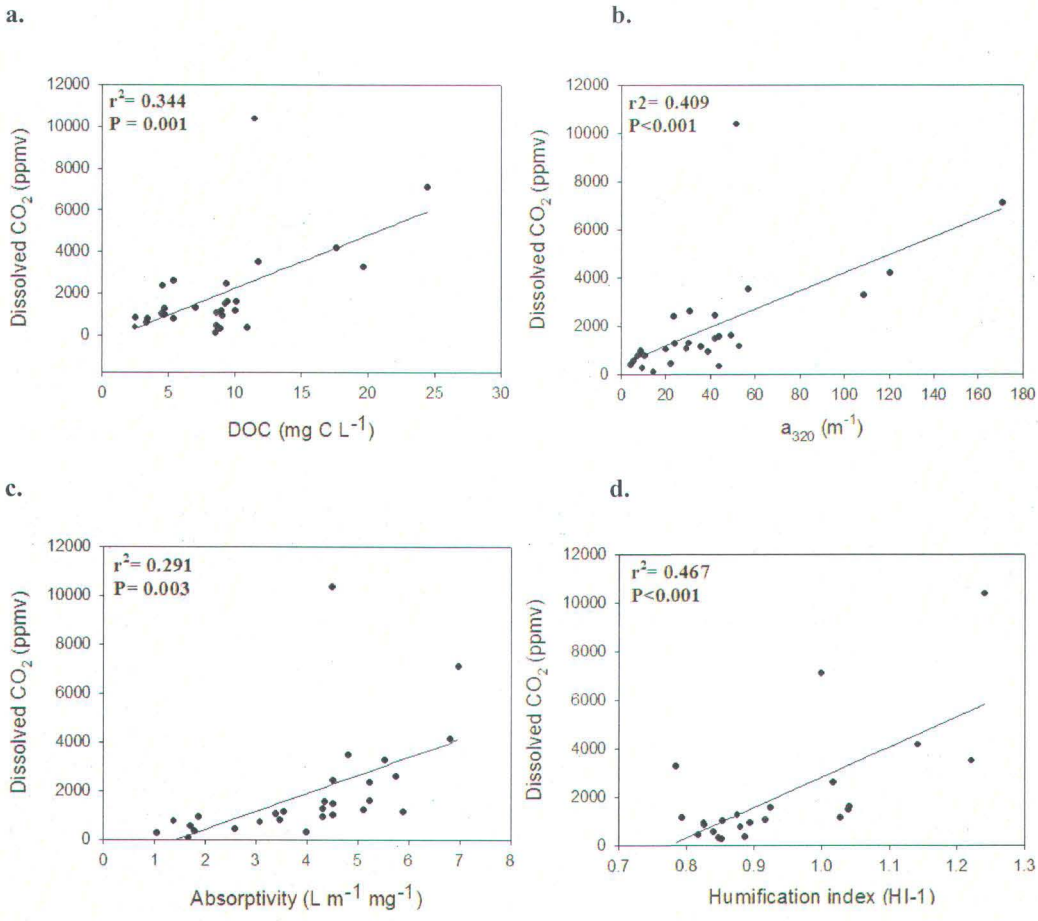
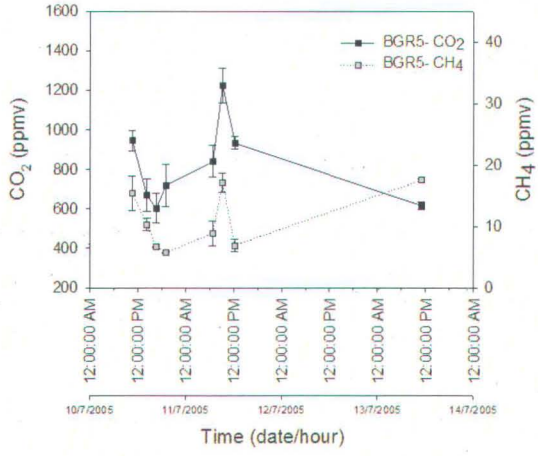


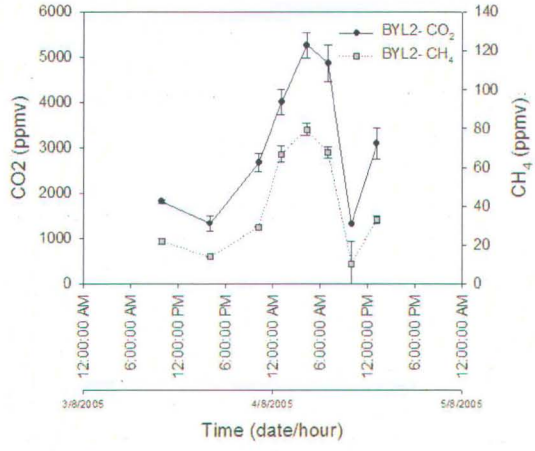
Figure 10: Diurnal variations in dissolved carbon dioxide (CO_2; filled squares) and methane (CH_4;emptied squares) in surface water of three thermokarst ponds. Standard deviations are shown for each data point (triplicata).

a. BGR5 surface water of a depressed lithalsa in discontinuous permafrost, **b.** BYL2 surface water of a periphery pond in continuous permafrost, **c**. BYL4 surface water on a depressed polygon in continuous permafrost. Note time that scales vary between BGR5 and the two BYL ponds.

a.



b.



c.

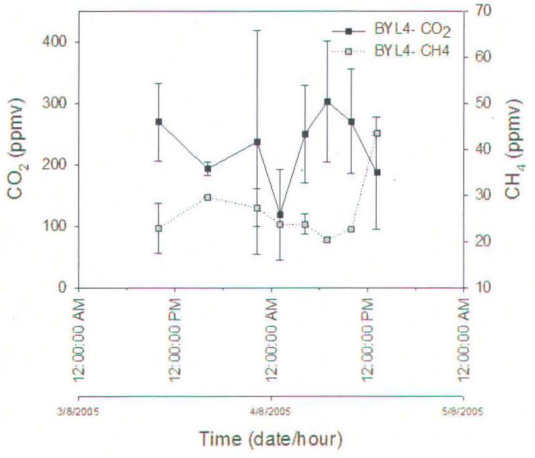


Figure 11: The relationship between bacterial abundance and nutrient concentrations in surface waters. a. ammonia concentration (NH4) in thermokarst ponds, b. total phosphorus

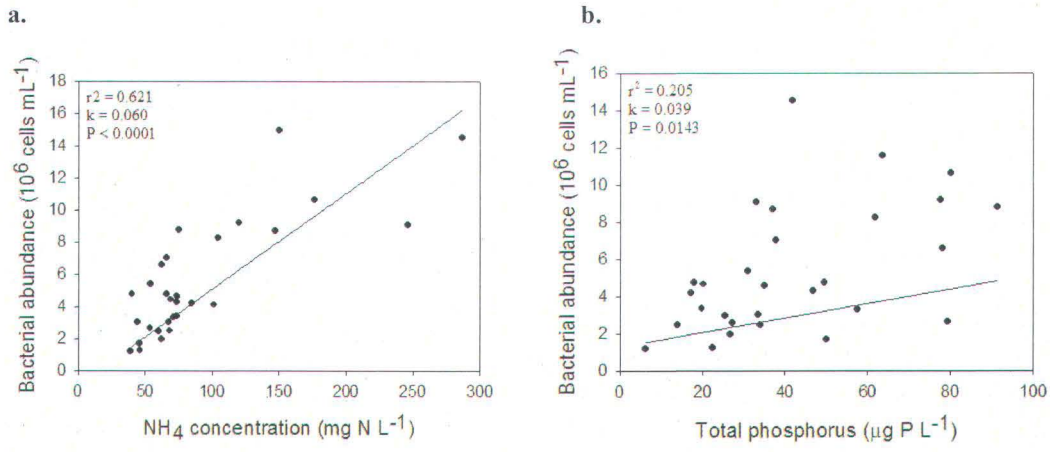


Figure 12: Bacterial production estimated from the incorporation of tritiated leucine with different addition treatments to determine nutrient limitation in two thermokarst ponds
a. BGR1, **b.** BGR5. The four treatments: control with no addition, P = addition of phosphate, C = addition of glucose, P + C = addition of both glucose and phosphate. Differences between treatments are indicated in the figures. Standard deviations are shown for each treatment (triplicate).

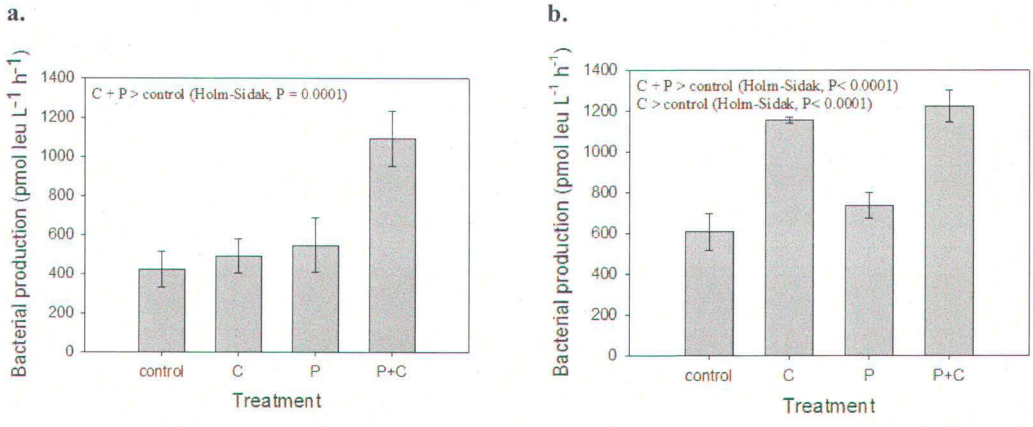


Figure 13: Photographs of two filled ponds at two different stage of filling.

Table 1: Physical characteristics of sampled thermokarst ponds during the 2004-2005 field campaign.

Site/Ecoregion	Latitude (N)	Type of pond*	Pond name	Date	0 m temp. (°C)	Max depth (m)
Umiujaq	56°36	d	bgr1 (2004)	04/07/2004	14.0	3.1
Sheldrake river		d	bgr1 (2005)	11/07/2005	20.9	3.3
(BGR)/shrub tundra		d	bgr2	04/07/2004	12.0	1.2
		p	bgr3	04/07/2004	11.5	n.a
		d	bgr4	06/07/2004	15.0	2.8
		d	bgr5 (2004)	06/07/2004	n.a	2.3
		d	bgr5 (2005)	11/07/2005	19.9	2.0
		d	bgr6	07/07/2004	n.a	3.5
		d	bgr7	07/07/2004	n.a	2.8
		d	bgr8	07/07/2004	16.0	2.1
		d	bgr9	12/07/2005	27.3	1.7
		d	bgr10	12/07/2005	28.1	1.6
		d	bgr12	13/07/2005	23.6	2.8
		p	bgr16	13/07/2005	n.a	n.a
		p	bgr32	15/07/2005	n.a	n.a
		p	bgr33	16/07/2005	n.a	n.a
Whapmagoostui-	55°19	d	kwk1	19/07/2005	24.2	2.2
Kuujjuarapik		d	kwk2	19/07/2005	24.1	3.0
Kwakwatanikapistikw		d	kwk3	01/07/2004	18.6	2.8
River		d	kwk4	01/07/2004	17.5	1.5
(KWK)/forest tundra		d	kwk5	18/07/2005	n.a	n.a
		d	kwk6	18/07/2005	n.a	n.a
		d	kwk7	18/07/2005	n.a	n.a
		d	kwk8	18/07/2005	n.a	n.a
		d	kwk9	01/07/2004	19.1	n.a
		d	kwk10	01/07/2004	20.5	n.a
Sasapimakwananistikw						
River	55°13	d	kuj1	01/07/2004	21.0	n.a
(KUJ)/forest tundra		d	kuj6	14/07/2004	20.5	1.0
Boniface river	57°30-44	p	bon1	20/07/2004	13.5	< 1
(BON)/forest tundra		p	bon2	20/07/2004	9.5	< 1
		p	bon4	21/07/2004	11.0	< 1
		p	bon5	24/07/2004	7.0	< 1
		p	bon8	25/07/2004	9.0	< 1
		p	bon9	26/07/2004	13.0	< 1
Bylot Island	72° 53-	d	byl1	29/07/2005	12.6	0.6
(BYL)/arctic tundra	73° 09	p	byl2	30/07/2005	7.1	0.3
		d	byl3	30/07/2005	13.2	0.1
		d	byl4	30/07/2005	12.4	0.3
		d	byl7	31/07/2005	9.7	n.a
		d	byl8	31/07/2005	n.a	n.a

(...continued)

Site/Ecoregion	Latitude (N)	Type of pond*	Pond name	Date	0 m temp. (°C)	Max depth (m)
Bylot Island (continued...) (BYL)/arctic tundra		p	byl11	03/08/2005	10.2	n.a
		p	byl12	02/08/2005	9.7	0.9
		p	byl13	02/08/2005	11.3	0.9
		p	byl14	02/08/2005	9.8	0.5
		d	byl15	02/08/2005	9.8	0.5
		d	byl16	02/08/2005	12.5	0.3
		d	byl17	02/08/2005	12.6	0.3
		p	byl18	02/08/2005	10.4	0.4
		d	byl20	06/08/2005	n.a	n.a
		p	byl21	06/08/2005	11.6	n.a
Amundsen Cruise Umiujaq (UMI)/shrub tundra	56°32	d	umi1	03/09/2004	7.9	n.a
		d	umi2	03/09/2004	8.8	n.a
		d	umi3	05/07/2004	10.0	1.5
Kangiqsualujjuaq (KAN)/shrub tundra	58° 41	d	aaq2	27/09/2004	3.2	n.a
		d	aaq3	27/09/2004	8.8	n.a
Whapmagoostui-Kuujjuarapik (KUUJJ) /forest tundra	55°18	d	kuujj2	01/09/2004	10.4	n.a
		d	kuujj3	01/09/2004	11.8	n.a
Boutin river (BOU)/forest tundra	55°49	d	bou1	22/07/2005	15.5	n.a
		d	bou2	22/07/2005	15.3	n.a

	Temp.	Depth
Minimum	3.2	0.1
Maximum	28.1	3.5
Median	12.5	1.5
Mean	14.1	1.6
Stdev	5.7	1.1
N	47	29

n.a = not available
*d= depression
p= periphery

Table 2: Physicochemical characteristics of some surrounding environment sampled in the vicinity of the thermokarst ponds.

Site	Latitude (° N)	Description	Name	Date	pH	TSS (mg L^{-1})	Name	Conductivity ($\mu S\ cm^{-1}$)	Dissolved O_2 (%)
Bylot Island	72° 53 to 73° 09	glacier rivers	BYL6	July 31, 2005	7.6	n.a	BYL6	18	103
			BYL9	July 31, 2005	n.a	n.a	BYL9	n.a	n.a
		Lakes	BYL10	August 1, 2005	7.6	1.0	BYL10	12	104
			BYL19	August 6, 2005	7.6	n.a	BYL19	92	106
Kwakwatanikapistikw river	55°19	River	riv. Kwak	July 19, 2005	7.0	n.a	riv. Kwak	45	104
		recolonized pond	KWK2-B	July 19, 2005	n.a	64.6	KWK2-B	n.a	n.a
Sasapimakwananistikw river	55°13	puddle with sphagnum	KUJ2	July 9, 2004	4.1	n.a	KUJ2	n.a	n.a
Boniface river	57°30	puddles with sphagnum	BON3	July 20, 2004	4.4	3.8	BON3	26	n.a
	57°44		BON6	July 24, 2004	4.5	1.3	BON6	29	n.a
			BON7	July 25, 2004	4.3	n.a	BON7	n.a	n.a
Amundsen cruise		standards ponds	INU3	September 7, 2004	7.8	n.a	INU3	177	n.a
		(rock ponds)	PUV2	September 11, 2004	6.2	n.a	PUV2	30	n.a
			SAL3	September 18, 2004	7.3	n.a	SAL3	101	n.a
			KAN2	September 19, 2004	6.3	n.a	KAN2	88	n.a
			TAS1	September 25, 2004	7.7	n.a	TAS1	30	n.a
		Minimum			4.1	1.0	min	12	103
		Maximum			7.8	64.6	max	177	106
		Median			7.0	2.6	med	30	104
		Mean			6.3	17.7	mean	59	104
		Stdev			1.5	31.3	stdev	50	1
		N			13	4	N	11	4

(...continued)

Name	Nutrients				Bacteria abundance	DOC	a_{CDOM} 320	Spectral slope (S)	a_{CDOM} absorptivity	FI[1]	Humification indice		Dissolved gas	
	NH_4 (µg N L^{-1})	NO_3 (µg N L^{-1})	TP (µg P L^{-1})	PO_4 (µg P L^{-1})	(10^6 cells mL^{-1})	(mg L^{-1})	(m^{-1})		(m^{-1} (mg L^{-1})$^{-1}$)		HI-1	HI-2	CO_2 ppmv	CH_4 ppmv
BYL6	46.7	0.26	791	1.89	n.a	0.2	0.86	0.013	3.60	n.a	0.89	0.54	n.a	n.a
BYL9	n.a	n.a	n.a	n.a	n.a	6.1	26.8	0.016	4.42	1.18	0.99	0.71	809	4
BYL10	55.9	0.03	15.9	<1	2.8	4.7	7.73	0.019	1.64	1.24	0.81	0.45	n.a	n.a
BYL19	n.a	n.a	n.a	n.a	1.3	6.2	24.8	0.016	3.98	1.18	1.03	0.74	n.a	n.a
riv. Kwak	n.a	n.a	n.a	n.a	n.a	7.5	33.9	0.015	4.54	1.11	1.01	0.76	n.a	n.a
KWK2-B	n.a	n.a	n.a	n.a	30.6	25.4	56.5	0.015	2.23	1.30	1.14	0.86	1757	35
KUJ2	n.a	n.a	n.a	n.a	13.9	41.6	218	0.017	5.25	1.13	1.07	1.06	n.a	n.a
BON3	110	n.a	54	4	4.6	28.7	152	0.015	5.30	1.21	1.17	1.17	n.a	n.a
BON6	n.a	n.a	n.a	2	4.2	31.3	156	0.015	5.00	1.28	1.08	0.90	3194	30
BON7	n.a	n.a	n.a	n.a	4.6	20.5	80.9	0.015	3.94	1.42	1.09	0.66	25182	15
INU3	n.a	n.a	n.a	2	4.5	7.8	19.3	0.016	2.48	1.22	0.99	0.81	n.a	n.a
PUV2	n.a	n.a	n.a	2	2.3	5.3	n.a	n.a	n.a	n.a	n.a	n.a	n.a	n.a
SAL3	n.a	n.a	n.a	5	1.1	6.8	28.1	0.016	4.16	1.19	1.09	0.91	n.a	n.a
KAN2	n.a	n.a	n.a	1	2.3	3.4	8.7	0.016	2.52	1.32	0.89	0.58	n.a	n.a
TAS1	n.a	n.a	n.a	5	1.2	7.2	16.1	0.018	2.24	1.17	0.91	0.59	n.a	n.a
Minimum	46.7	0.0	15.9	1.0	1.1	0.2	0.86	0.013	1.64	1.1	0.8	0.5	809	4.4
Maximum	110.0	0.3	791	5.0	30.6	41.6	218.2	0.019	5.30	1.4	1.2	1.2	25182	35.3
Median	54.9	0.1	53.7	2.0	3.5	7.2	27.5	0.016	3.96	1.2	1.0	0.8	2475	22.6
Mean	70.5	0.1	287	2.9	6.1	13.5	59.3	0.016	3.66	1.2	1.0	0.8	7735	21.2
stdev	34.4	0.2	437	1.6	8.4	12.6	67.8	0.001	1.23	0.1	0.1	0.2	11672	14.2
N	3	2	3	8	12	15	14	14	14	13	14	14	4	4

Table 3: DOM characterizations of sampled thermokarst ponds during 2004-2005 field campaign.

Pond name	DOC	a_{CDOM} 320 nm	Spectral slope (S)	Absorptivity a_{CDOM}	FI[1]	Humification index[2]	
	(mg L^{-1})	(m^{-1})		m^{-1} (mg L^{-1})$^{-1}$		HI-1	HI-2
bgr1 (2004)	3.3	5.71	0.014	1.71	1.35	0.84	0.45
bgr1 (2005)	2.5	4.46	0.015	1.79	1.36	0.89	0.50
bgr2	3.0	12.9	0.014	4.33	1.18	1.00	0.84
bgr3	5.4	30.8	0.015	5.75	1.14	1.02	0.95
bgr4	2.5	8.74	0.015	3.48	1.27	0.83	0.52
bgr5 (2004)	1.3	5.88	0.013	4.63	1.24	0.86	0.51
bgr5 (2005)	4.7	8.79	0.014	1.87	1.18	0.83	0.51
bgr6	4.3	22.5	0.015	5.25	1.17	0.94	0.69
bgr7	1.3	5.42	0.012	4.08	1.30	0.79	0.46
bgr8	9.0	52.9	0.015	5.89	n.a	1.03	0.93
bgr9	2.7	5.75	0.014	2.11	1.24	0.83	0.49
bgr10	5.1	26.7	0.015	5.23	1.15	0.90	0.60
bgr12	4.3	4.03	0.016	0.94	1.18	0.84	0.53
bgr16	9.8	28.6	0.015	2.92	n.a	0.88	0.48
bgr32	7.3	24.5	0.016	3.35	1.12	0.97	0.77
bgr33	11.5	69.1	0.015	6.01	1.16	0.92	0.68
kwk1	9.0	38.9	0.015	4.31	1.13	0.89	0.61
kwk2	7.1	30.5	0.014	4.32	1.14	0.88	0.58
kwk3	3.4	10.5	0.013	3.08	n.a	n.a	n.a
kwk4	5.9	178.6	0.011	30.1[3]	1.34	0.61	0.27
kwk5	9.3	42.0	0.015	4.51	1.15	1.04	0.83
kwk6	5.4	7.46	0.016	1.38	1.16	0.88	0.67
kwk7	8.6	29.23	n.a	3.40	1.16	0.92	0.58
kwk8	10.1	44.00	0.015	4.35	1.15	0.92	0.61
kwk9	4.5	20.17	0.015	4.51	1.23	0.85	0.54
kwk10	4.5	65.6	0.015	5.69	1.19	0.89	0.54
kuj1	24.5	170.8	0.014	6.98	1.24	1.00	0.85
kuj6	26.0	23.8	0.013	5.24	n.a	n.a	n.a
bon1	17.6	120.2	0.014	6.82	1.25	1.14	1.03
bon2	11.5	51.40	0.015	4.49	1.18	1.24	1.44
bon4	9.3	42.23	0.015	4.52	n.a	n.a	n.a
bon5	9.4	49.45	0.015	5.24	1.18	1.04	0.90
bon8	11.8	56.79	0.016	4.81	1.19	1.22	1.28
bon9	20.6	108.9	0.015	5.29	1.28	1.14	0.97
byl1	9.4	20.9	0.016	2.23	1.20	0.85	0.52
byl2	19.7	108.8	0.015	5.53	1.31	0.79	0.38

(...continued)

Pond name	DOC	a_{CDOM} 320 nm	Spectral slope (S)	DOC-specific a_{CDOM}	FI[1]	Humification index[2]	
						HI-1	HI-2
	(mg L^{-1})	(m^{-1})		m^{-1} (mg L^{-1})$^{-1}$		*400/360*	*470/360*
byl3	16.7	88.4	0.015	5.30	1.23	0.83	0.52
byl4	11.0	43.9	0.016	4.00	1.21	0.85	0.49
byl7	16.9	28.2	0.018	1.67	1.27	0.72	0.35
byl8	10.6	25.0	0.016	2.37	1.24	0.77	0.42
byl11	21.5	92.7	0.016	4.31	1.29	0.78	0.40
byl12	10.1	35.7	0.016	3.55	1.25	0.79	0.42
byl13	10.5	33.6	0.016	3.21	1.26	0.80	0.42
byl14	8.6	22.3	0.017	2.60	1.23	0.82	0.47
byl15	7.9	19.6	0.016	2.49	1.21	0.86	0.54
byl16	8.6	14.4	0.018	1.68	1.26	n.a	n.a
byl17	10.1	19.3	0.016	1.91	1.23	0.77	0.45
byl18	11.0	42.3	0.016	3.85	1.27	0.83	0.47
byl20	6.8	17.8	0.017	2.61	1.26	0.86	0.51
byl21	n.a	n.a	n.a	n.a		n.a	n.a
umi1	2.0	6.9	0.017	3.52	1.17	1.20	1.02
umi2	2.8	n.a	n.a	n.a	1.17	n.a	n.a
umi3	4.7	23.9	0.015	5.11		n.a	n.a
aaq2	10.0	42.9	0.016	4.30	1.20	1.02	0.92
aaq3	11.2	52.9	0.015	4.73	1.22	1.04	0.85
kuujj2	11.5	75	0.015	5.83	1.18	1.13	0.94
kuujj3	12.9	n.a	n.a	n.a	1.17	0.99	0.77
bou1	3.3	3.1	0.017	0.93	n.a	1.04	0.77
bou2	7.0	24.8	0.016	3.55	n.a	0.99	1.02

	DOC	a_{320}	S	Absorptivity	FI	Humification index	
Minimum	1.3	3.1	0.011	0.93	1.12	0.61	0.27
Maximum	26.0	178.6	0.018	6.98	1.36	1.24	1.44
Median	8.8	28.4	0.015	4.30	1.21	0.88	0.56
Mean	9.0	40.2	0.015	3.88	1.22	0.92	0.66
Stdev	5.7	38.3	0.001	1.52	0.06	0.13	0.25
N	58.0	56	55	55	50	52	52

[1] MacKnight et al. 2001

[2] Kalbitz et al. 1999

[3] Not counted

n.a = not available

Table 4: Chemical characteristics of sampled thermokarst ponds during the 2004-2005 field campaign.

Pond name	pH*	TSS solids ($mg\ L^{-1}$)	Conductivity ($\mu S\ cm^{-1}$)	Dissolved O_2 (%)	Nutrients			
					NH_4	NO_3	TP	PO_4
					($\mu g\ N\ L^{-1}$)		($\mu g\ P\ L^{-1}$)	
bgr1 (2004)	6.9	23.8	46	n.a	66.0	n.a	49.5	29
bgr1 (2005)	7.1	5.3	n.a	106	62.2	21.0	26.7	2.0
bgr2	6.4	271	252	120	101	n.a	285	n.a
bgr3	6.5	14.5	16	99	n.a	n.a	n.a	n.a
bgr4	7.0	39.7	23	102	62.0	n.a	78.1	45
bgr5 (2004)	n.a	n.a	18	n.a	n.a	n.a	n.a	n.a
bgr5 (2005)	6.4	15.5	n.a	97	n.a	n.a	63.4	n.a
bgr6	n.a	n.a	n.a	n.a	n.a	n.a	n.a	n.a
bgr7	n.a	n.a	n.a	n.a	n.a	n.a	n.a	n.a
bgr8	6.8	n.a	n.a	n.a	120	n.a	77.6	14
bgr9	8.5	n.a	110	122	n.a	n.a	n.a	n.a
bgr10	7.3	n.a	41	114	n.a	n.a	n.a	n.a
bgr12	7.0	n.a	32	104	n.a	n.a	n.a	n.a
bgr16	n.a	n.a	n.a	n.a	n.a	n.a	n.a	n.a
bgr32	n.a	n.a	n.a	n.a	n.a	n.a	n.a	n.a
bgr33	n.a	n.a	n.a	n.a	n.a	n.a	n.a	n.a
kwk1	6.9	9.4	31	95	53.5	10.8	79.3	2.9
kwk2	6.4	3.9	30	93	45.3	46.5	49.9	3.0
kwk3	7.1	7.8	31	n.a	66	n.a	37.8	10
kwk4	7.1	159	28	n.a	150	n.a	n.a	278
kwk5	n.a	n.a	n.a	n.a	n.a	n.a	n.a	n.a
kwk6	n.a	n.a	n.a	n.a	n.a	n.a	n.a	n.a
kwk7	n.a	n.a	n.a	n.a	n.a	n.a	n.a	n.a
kwk8	n.a	n.a	n.a	n.a	n.a	n.a	n.a	n.a
kwk9	7.0	2.8	35	n.a	147	n.a	36.9	10
kwk10	n.a	12.4	32	n.a	44	n.a	33.5	14
kuj1	5.8	5.4	50	n.a	176	n.a	80.0	4.0
kuj6	6.9	11.4	56	n.a	287	n.a	41.8	2.0
bon1	5.2	11.4	20	n.a	104	n.a	61.8	11
bon2	5.1	1.3	15	n.a	40	n.a	18.0	4.0
bon4	5.1	3.5	14	n.a	46	n.a	22.5	1.0
bon5	5.1	n.a	19	n.a	n.a	n.a	n.a	n.a
bon8	5.1	0.7	18	n.a	39	n.a	6.2	4.0
bon9	5.1	7.3	22	n.a	54	n.a	30.9	4.0
byl1	9.2	2.0	48	116	67.2	60.6	25.4	<1
byl2	7.4	2.8	99	100	100.4	24.8	27.3	4.3
byl3	7.5	10.4	27	141	73.5	36.8	46.7	3.4
byl4	7.7	4.9	35	122	74.6	378.2	91.3	<1
byl7	8.8	24.0	111	111	71.1	959.0	57.4	2.0
byl8	n.a	11.6	n.a	n.a	73.8	46.7	35.0	1.5
byl11	7.4	7.0	45	133	68.3	n.a	33.9	2.4

(…continued)

Pond name	pH*	TSS solids (mg L^{-1})	Conductivity ($\mu S\ cm^{-1}$)	Dissolved O_2 (%)	Nutrients NH_4 ($\mu g\ N\ L^{-1}$)	NO_3	TP ($\mu g\ P\ L^{-1}$)	PO_4
byl12	7.4	2.3	171	101	73.6	n.a	19.8	1.9
byl13	7.5	3.4	205	117	n.a	n.a	n.a	n.a
byl14	8.0	0.4	45	105	73.2	n.a	20.1	<1
byl15	8.0	1.7	99	105	n.a	n.a	n.a	n.a
byl16	9.1	1.0	56	114	84.4	n.a	17.3	1.6
byl17	8.7	5.0	48	110	n.a	n.a	n.a	n.a
byl18	7.4	5.4	108	78	246	n.a	32.9	4.3
byl20	n.a	n.a	n.a	n.a	n.a	n.a	n.a	n.a
byl21	7.0	n.a	57	100	n.a	n.a	n.a	n.a
umi1	7.4	n.a	28	n.a	n.a	n.a	n.a	2.0
umi2	6.9	n.a	27	n.a	n.a	n.a	n.a	3.0
umi3	6.6	2.0	21	n.a	60.0	n.a	13.9	3.0
aaq2	7.0	n.a	60	n.a	n.a	n.a	n.a	3.0
aaq3	6.7	n.a	26	n.a	n.a	n.a	n.a	3.0
kuujj2	6.2	n.a	33	n.a	n.a	n.a	n.a	n.a
kuujj3	6.9	n.a	37	n.a	n.a	n.a	n.a	4.0
bou1	7.3	n.a	17	n.a	n.a	n.a	n.a	n.a
bou2	6.8	n.a	24	n.a	n.a	n.a	n.a	n.a

	pH*	TSS	Conductivity	DO	NH_4	NO_3	TP	PO_4
Minimum	5.1	0.4	14	78	39.0	10.8	6.2	1.0
Maximum	9.2	271	252	141	287	959	285	278
Median	7.0	5.4	33	106	72.2	46.5	35.9	3.4
Mean	7.0	20.3	53	108	91.0	176	50.0	15.4
Stdev	1.0	52.0	50	14	58.4	315	49.8	49.6
N	46	34	45	24	30	9	30	31

n.a = not available

*arbitrary choice of a value among many profiles

Table 5: Results of bathymetric soundings of five thermokarst ponds (principal ponds)

Site	Pond	Maximum depth (m)	Maximum length (m)	Maximum width(m)	Surface area (m^2)	Volume (m^3)
BGR	bgr1	3.3	29.0	18.5	523	872
	bgr5	2.0	23.0	16.0	350	487
KWK	kwk1	2.2	28.0	17.0	384	511
	kwk2	3.0	36.0	19.0	511	720
BYL	byl1	0.5	28.0	15.0	~322	n.a

Table 6: Comparison of surface and bottom waters chemical characteristics in five thermokarst ponds.

Pond name	Conductivity ($\mu S\ cm^{-1}$)		Dissolved oxygen (%)	($mg\ L^{-1}$)	(%)	($mg\ L^{-1}$)	NH_4 ($\mu g\ N\ L^{-1}$)		TP $\mu g\ P\ L^{-1}$	
	surface	*Bottom*	*surface*	*surface*	*bottom*	*bottom*	surface	*bottom*	surface	*bottom*
bgr1 (2005)	n.a	n.a	106	9.44	1.1	0.13	62.2	68.6	26.7	n.a
bgr5 (2005)	n.a	n.a	97	8.83	1.4	0.18	n.a	n.a	63.4	n.a
kwk1	31	43	95	8.00	1.5	0.18	53.5	n.a	79.3	297
kwk2	30	96	93	7.77	1.6	0.20	45.3	n.a	49.9	393
byl11	45	175	133	14.3	64.8-45.0	7.48-5.34	68.3	116	33.9	622

	Conductivity		DO				NH_4		TP	
Minimum	30	43	93	7.77	1.1	0.13	45.3	68.6	26.7	297
Maximum	45	175	133	14.3	1.6	0.20	68.3	116	79.3	622
Median	31	96	97	8.83	1.5	0.18	57.9	92.1	49.9	393
Mean	35	105	105	9.66	1.4	0.17	57.3	92.1	50.6	437
stdev	8	66	16	2.67	0.2	0.03	10.1	33.2	21.4	167
N	3	3	5	5	4	4	4	2	5	3

(…continued)

Pond name	PO_4 $\mu g\ P\ L^{-1}$		Bacteria abundance 10^6 cells mL^{-1}		DOC $mg\ L^{-1}$		a_{320}		Spectral slope (S)	
	surface	*bottom*	*surface*	*bottom*	*surface*	*bottom*	*surface*	*bottom*	*surface*	*bottom*
bgr1 (2005)	2.0	18.5	1.98	4.43	2.49	2.48	4.46	2.15	0.015	n.a
bgr5 (2005)	n.a	n.a	11.6	n.a	4.70	3.01	8.79	8.99	0.014	0.016
kwk1	2.9	n.a	2.65	13.7	9.04	8.92	38.9	42.5	0.015	0.015
kwk2	3.0	n.a	1.71	1.98	7.07	6.77	30.5	35.5	0.014	0.014
byl11	2.4	12.6	2.49	20.9	21.5	39.4	92.7	648	0.016	0.013

	PO4		Bacteria abundance		DOC		a_{320}		Spectral slope (S)	
Minimum	2.0	12.6	1.71	1.98	2.5	2.5	4.5	2.1	0.014	0.013
Maximum	3.0	18.5	11.6	20.9	21.5	39.4	92.7	648	0.016	0.016
Median	2.6	15.6	2.49	9.04	7.1	6.8	30.5	35.5	0.015	0.015
Mean	2.6	15.6	4.09	10.2	9.0	12.1	35.1	147	0.015	0.015
stdev	0.4	4.2	4.2	8.7	7.4	15.5	35.3	280	0.001	0.001
N	4	2	5	4	5	5	5	5	5	4

(…continued)

Pond name	DOC-specific a_{CDOM} m^{-1} $(mg\ L^{-1})^{-1}$		FI[1]		Humification index[2] *HI-2*		CO_2 ppmv	Ppmv	CH_4 ppmv	ppmv
	surface	*bottom*	*surface*	*bottom*	*surface*	*bottom*	*surface*	*bottom*	*surface*	*bottom*
bgr1 (2005)	1.79	0.87	1.36	1.38	0.50	0.53	364	3089	10.0	23.9
bgr5 (2005)	1.87	2.98	1.18	1.23	0.51	0.71	949	9258	19.5	1253
kwk1	4.31	4.76	1.13	1.19	0.61	0.87	926	15235	18.5	2309
kwk2	4.32	5.25	1.14	1.22	0.58	0.70	1283	17382	37.1	3571
byl11	4.31	16.43	1.29	1.96	0.40	0.11	n.a	n.a	n.a	n.a
	DOC-specific a_{CDOM}		FI		HI-2		CO_2		CH_4	
Minimum	1.79	0.87	1.13	1.19	0.40	0.11	364	3089	10.0	23.9
Maximum	4.32	16.4	1.36	1.96	0.61	0.87	1282	17382	37.1	3571
Median	4.31	4.76	1.18	1.23	0.51	0.70	938	12247	19.0	1781
Mean	3.32	6.06	1.22	1.40	0.52	0.58	881	11241	21.3	1789
stdev	1.36	6.0	0.10	0.32	0.08	0.29	381	6430	11.4	1511
N	5	5	5	5	5	5	4	4	4	4

Table 7: Biological components and concentrations of dissolved gases in thermokarst ponds

Pond name	Bacteria abundance	Chlorophylle *a*	Dissolved gas	
			CO_2	CH_4
	(10^6 cells mL^{-1})	($\mu g\ L^{-1}$)	(ppmv)	(ppmv)
bgr1 (2004)	4.8	2.3	567	5.4
bgr1 (2005)	2.0	0.4	364	10.0
bgr2	4.1	n.a	2056	19.5
bgr3	7.0	1.3	2608	33.0
bgr4	6.6	4.6	835	5.6
bgr5 (2004)	3.2	n.a	n.a	n.a
bgr5 (2005)	11.6	0.3	949	19.5
bgr6	8.9	0.8	n.a	n.a
bgr7	3.7	1.2	n.a	n.a
bgr8	9.2	6.7	1158	32.3
bgr9	4.2	n.a	n.a	n.a
bgr10	3.4	n.a	n.a	n.a
bgr12	3.9	n.a	n.a	n.a
bgr16	15.6	n.a	n.a	n.a
bgr32	9.4	n.a	n.a	n.a
bgr33	3.9	n.a	n.a	n.a
kwk1	2.7	3.7	926	18.5
kwk2	1.7	1.8	1283	37.1
kwk3	7.0	2.0	750	4.0
kwk4	15.0	n.a	842	1.1
kwk5	7.5	n.a	1470	17.2
kwk6	4.1	n.a	757	10.7
kwk7	10.2	n.a	1048	53.8
kwk8	7.6	n.a	1564	20.9
kwk9	8.7	3.3	1028	10.3
kwk10	3.0	1.1	n.a	n.a
kuj1	10.6	6.2	7106	6.8
kuj6	14.5	4.9	2370	17.6
bon1	8.3	5.0	4166	11.6
bon2	4.8	0.4	10381	63.7
bon4	1.3	3.7	2442	20.7
bon5	5.9	0.6	1603	33.2
bon8	1.2	0.4	3498	25.8
bon9	5.4	8.8	n.a	n.a
byl1	3.0	1.1	275	10.1
byl2	2.6	2.7	3259	38.7
byl3	4.3	n.a	680	22.2
byl4	8.8	5.0	321	39.4
byl7	3.3	n.a	n.a	n.a
byl8	4.6	n.a	n.a	n.a

(…continued)

Pond name	Bacteria abundance	Chlorophylle *a*	Dissolved gas	
			CO_2	CH_4
	(10^6 cells mL^{-1})	(µg L^{-1})	(ppmv)	(ppmv)
byl11	2.5	2.7	n.a	n.a
byl12	3.4	n.a	1132	11.6
byl13	4.7	n.a	n.a	n.a
byl14	4.7	n.a	440	10.3
byl15	5.7	n.a	n.a	n.a
byl16	4.2	n.a	86	7.5
byl17	2.9	0.8	n.a	n.a
byl18	9.1	n.a	n.a	n.a
byl20	0.9	n.a	n.a	n.a
byl21	1.5	2.5	n.a	n.a
umi1	0.7	0.4	n.a	n.a
umi2	2.5	0.8	n.a	n.a
umi3	2.5	0.9	1249	0.9
aaq2	4.9	1.9	n.a	n.a
aaq3	16.8	n.a	n.a	n.a
kuujj2	4.8	3.4	n.a	n.a
kuujj3	12.3	4.4	n.a	n.a
bou1	8.1	n.a	n.a	n.a
bou2	8.7	n.a	n.a	n.a

	BA	Chl *a*	CO_2	CH_4
Minimum	0.7	0.3	86	0.9
Maximum	16.8	8.8	10381	63.7
Median	4.7	2.0	1132	17.6
Mean	5.9	2.6	1846	20.0
stdev	3.9	2.1	2131	15.2
N	59.0	33.0	31	31.0

n.a = not available

Tableau 8: Bacterial production estimated by leucine incorporation

Pond	date	depth	fraction T= total <3 µm	in situ temp. °C	incubation temp. °C	Leucine incorporation pmol leu L^{-1} h^{-1}	Standard Deviation pmol leu L^{-1} h^{-1}
BGR1	July 11, 2005	s	T	30	21	529	27
	July 11, 2005	s	<3	30	21	98	16
	July 11, 2005	b	T	20	21	1078	76
	July 11, 2005	b	<3	20	21	0	0
BGR5	July 11, 2005	s	T	30	20	1195	41
	July 11, 2005	s	<3	30	20	523	22
	July 11, 2005	b	T	20	20	1260	54
	July 11, 2005	b	<3	20	20	0	0
BGRA	July 12, 2005	s	T	25	27	192	9
BGRB	July 12, 2005	s	T	25	28	305	8
BGR12	July 13, 2005	s	T	22	24	103	8
BGR16	July 13, 2005	s	T	22	25	720	25
BGR32	July 13, 2005	s	T	22	25	190	32
KWK 1	July 18, 2005	s	T	24	24	243	14
	July 19, 2005	b	T	8	15	167	30
KWK 2	July 18, 2005	s	T	24	26	203	34
	July 19, 2005	b	T	8	17	523	57
KWK 5	July 18, 2005	s	T	24	23	254	18
KWK 6	July 18, 2005	s	T	24	23	413	20
KWK 7	July 18, 2005	s	T	24	23	364	19
KWK 8	July 18, 2005	s	T	24	24	359	19

s= surface
b= bottom

CHAPITRE 3: Microbial and photochemical transformation of dissolved organic matter in thermokarst ponds: implications for global carbon cycling.

Résumé *(Dégradation photochimique et microbienne de la matière organique dissoute dans les mares de thermokarst: implication sur le cycle du carbone)*
Des expériences de dégradation photochimique et microbienne de la matière organique dissoute (MOD) ont été effectuées en 2005 sur 5 des mares qui ont fait l'objet d'une caractérisation dans le chapitre précédent. Les résultats d'une expérience préliminaire de dégradation microbienne effectuée en 2004 sur 2 mares supplémentaires sont aussi présentés. La MOD a été caractérisée par sa concentration (carbone organique dissout: COD), par spectrophotométrie (absorbance de la MOD chromophorique: MODC) et par spectrofluorimétrie (émission à 370 nm et fluorescence synchrone), et la croissance bactérienne a été mesurée lors d'incubation sous lumière naturelle (dégradation photochimique) et au noir (dégradation microbienne). Une portion significative de la MOD s'est dégradée autant par des processus photochimiques (5-14 % COD; 70-320 h) qu'en présence des assemblages microbiens naturels (14-30 % COD; 140 j). La quantité de MOD dégradée est comparable aux résultats obtenus dans d'autres milieux d'eau douce. La dégradation photochimique est un processus plus rapide de transformation de la MOD (6 à 26 fois plus rapide en moyenne dans les mares de thermokarst étudiées). La prédominance terrestre de la MOD (considérée moins labile) laisse croire que sa dégradation photochimique pourrait augmenter sa bio-disponibilité pour les communautés bactériennes. En effet, dans certains cas, la fluorescence de la MOD indiquait une transformation photochimique vers une composition plus riche en petites molécules. La formation de ce milieu limnétique semble favorable à la mobilisation du carbone stocké dans le sol vers le réseau alimentaire microbien puis en partie vers l'atmosphère.

Abstract

Microbial and photochemical degradation of dissolved organic matter (DOM) experiments were performed in 2005 on five ponds which have been characterized in the preceding chapter. Results from a preliminary microbial degradation experiment in 2004 on two additional ponds are also presented. DOM has been characterised by different means: concentration (dissolved organic carbon: DOC), spectrophotometry (chromophoric DOM absorption: CDOM) and spectrofluorimetry (emission scans and synchronous fluorescence). Bacterial growth has also been measured during incubation under natural light (photochemical degradation) and in the dark (microbial degradation). Significant fractions were degraded by photochemical processes (5-14 % of DOC; 70-320 h) and in presence of a fraction of natural bacteria assemblages (14-30 % of DOC; 140 d). The quantity of mineralized DOM is similar to that observed in other freshwater environments. Photochemical processes of degradation were faster than microbial degradation (6 to 26 times faster in our experimental ponds). DOM of predominant terrestrial origin has generally increased its lability to microbes after photolysis. Indeed, in most cases, DOM fluorescence indicated a photochemical degradation leading to a richer composition in smaller molecules. The formation of this new aquatic environment seems to be favourable for the mobilization of carbon to the microbial food web and to the atmosphere.

Introduction

Thermokarst processes occur as a result of permafrost thermodynamic changes. The processes involved include thawing, ponding, drainage, surface subsidience and erosion (**Yoshikawa & Hinzman 2003**). Ponding occurs when the permafrost is warm enough to start the melting of the ice and creates depressions where the water cannot drain away (as a result of soil properties or remaining permafrost beneath). Recent climate changes have already initiated the melting of permafrost in boreal and subarctic regions (**Luoto & Seppälä 2003, Payette et al. 2004**). According to climate models, vast extents of permafrost are likely to disappear from polar and subpolar regions (**Anisimov and Nelson 1997; Zhang et al. 2003; Sazonova et al. 2004**; **Lawrence and Slater 2005**). There is mounting evidence that recent climate warming is associated with permafrost thaw and consequent terrain effects (**Payette et al. 2004; Jorgenson et al. 2006**).

When a thermokarst pond is formed, the organic matter stocked in permafrost and peat can be mobilized in the water as dissolved organic matter (DOM) or particulate organic matter (POM). Since permafrost is a large carbon reservoir (**Zimov et al. 2006**), the potential of organic matter mobilization is huge and may play an important role in the global carbon cycle of the planet. For example, **Zimov et al. (2006)** estimated the potential carbon reservoir in frozen yedoma, which covers more than one million km^2 of the north plains of Siberia and Central Alaska, to an average depth of ~25 m, to be ~500 Gt in Siberia only. Another ~400 Gt of carbon are contained in non-yedoma permafrost (excluding peatlands). A range of 60 to 190 Gt were estimated to be stocked in Canadian permafrost (**Hobbie et al. 2000**). With as much as 43% of its area affected by permafrost, the potential for carbon mobilisation in thermokarst ponds through climate warming is high.

In our study, we were particularly interested in the fate of the dissolved organic matter liberated in aquatic systems when permafrost is melting. Organic material is not conservative in freshwater systems but rather undergoes various biological and photochemical transformations before a fraction of DOM is eventually discharged into the oceans (**Miller and Zepp 1995**: river and salt marsh; **Amon and Benner 1996**: river; **Opsahl and Benner 1998**: river and open-ocean; **Tranvik 1998:** lakes; **Retamal et al. 2006** arctic river). The newly mobilized DOM in thermokarst pond has two potential fates: it can be recalcitrant or transformed by diverse processes. If recalcitrant, the DOM will eventually end up in the drainage network as the result of pond drainage after the complete thawing of permafrost. If transformed, the DOM might

eventually be released as CO_2 and CH_4 to the atmosphere (photolysis or respiration) or transformed into other components through microbial and photochemical processes. In both cases, it raises concerns because of the important implications of increased carbon inputs to the ocean and atmosphere.

It is well known that DOM is the major form of organic matter in almost all aquatic ecosystems (**Findlay and Sinsabaugh 2003**). Moreover, DOM plays an important role in shaping aquatic ecosystems. Its concentration and composition both directly and indirectly influence the biology (e.g., microbial and plankton ecology, **Williamson et al. 2001, Wissel et al. 2003**), chemistry (trace metal speciation and transport, **Berault et al. 1996**; polycyclic aromatic carbon toxicity, **Diamond et al. 2000**) and physics (**Markager and Vincent 2000:** optical properties, **Fee et al. 1996**: thermal structure) of aquatic environments. Moreover, its importance for nutrient cycles (including carbon) in terrestrial ecosystems is well recognized (e.g. **Perakis and Hedin 2002; Cleveland et al. 2004**).

Photochemical and microbial processes that induce changes in natural DOM can influence many aspects of carbon cycling in aquatic environment. For example, microbial utilisation of dissolved organic carbon (DOC) may be an important source of new particulate carbon, which can be transferred to subsequent trophic levels (**Azam et al. 1983**). Bacterial respiration of DOM is the major component of total respiration in many environments (**Del Giorgio et al. 1996**). The bacterial utilization of the energy and carbon stored in the heterogenous, recalcitrant humic substances is poorly understood. Because of their relatively high molecular weight (HMW), humic substances must be degraded into smaller units before they can be utilized by bacterial cells (**Bertilsson and Tranvik 1998**). However, there are alternative mechanisms that render the some HMW organic material less refractory and thereby facilitate its utilization. For example, bacteria employ extracellular enzymes to cleave some macromolecules like proteins and polysaccharides into monomers or oligomers that are subsequently easily transported across the cell membrane (**Chròst 1991**). Also, the alteration of DOM exposed to natural sunlight produce a variety of biologically labile photoproducts (**Kieber et al. 1989, Mopper et al. 1991, Moran et Zepp 1997, Tranvik 1988**). Photomineralization and phototransformation directly remove and structurally alter DOM, influencing its biological utilization and fate in a complicated manner (**review from Mopper and Kieber 2002**). **Benner and Biddanda (1998)** showed that exposure of ocean's surface-water to sunlight resulted in a 75% reduction in bacterial production, whereas exposure of deep-water (15 m) DOM resulted in a 40% enhancement in bacterial production.

Enhanced bacterial growth in irradiated deep water samples was consistent with previous studies demonstrating the photoproduction of bioavailable substrates from deep-water DOM. On the other hand, UV radiation may cause a loss of carbon substrates for the microbial food web by photo-oxidizing organic material to dissolved inorganic carbon (**Bertilsson & Tranvik 2000**), and by initiating condensation reactions that decrease the biological availability of some organic compounds (**Obernosterer et al. 1999**). Interactions between biological and photochemical processes in the degradation of DOC can be viewed not only as a potential source of additional substrates for microbes, but also as a way to remineralize DOC with otherwise extremely long turn-over (**Moran et al. 1999**). To our knowledge, the literature describing the fate of DOM at high latitudes is sparse compared to temperate regions and is completely absent in the case of thermokarst ponds. As the latter have a high sensitivity to climate change, DOM fate in northern ecosystems like thermokarst ponds should arouse interest.

Understanding the dynamics of the DOC pool is a prerequisite for modelling the global carbon cycle (**Sóndergaard and Middelboe 1995**). In the present study, we monitored photochemical and microbial transformations of DOM in the surface water of thermokarst ponds. Waters in these ponds presents very different optical conditions and shelter an active microbial food web. This changing environment represents a good system to study the photochemical and microbial transformations of organic matter. The study was undertaken as a part of a broader program to examine the evolution of this overlooked ecosystem in regard to recent climatic changes and the role of permafrost degradation on carbon transfer from the tundra to the atmosphere and aquatic systems. For this purpose, extensive sampling of 57 ponds during the summers of 2004 and 2005 was carried out to describe the physical, chemical and biological properties of thermokarst ponds situated at different sites and latitudes (see **Chapter 2**). In the present chapter, we focus on the results of microbial and photochemical experiments performed on 5 of these ponds (7 for microbial degradation assays).

Materials and Methods

Study sites

In summer 2004 and 2005 (July to August), we sampled the water from ponds located at sites with different ecological and geological characteristics: three in Nunavik (Whapmagoostui-Kuujjuarapik N55.2° W77.3°, Boniface N57.4° W76.1° and Umiujaq N55.3° W76.1°) and one in Nunavut (Bylot Island Sirmilik National Park N73.2° W79.5°). Sites will be called KWK

(Kuujjuarapik), BGR (Umiujaq) and BYL (Bylot Island) to simplify, and the different ponds KWK1, KWK2, KWK3, BON4, BGR1, BGR5 and BYL1 (*see* **Table 9** for a description of the ponds). The five ponds sampled in 2005 were studied in more detail than the two ponds sampled in 2004. A more complete description of each site and a variety of other ponds in these areas can be found in the preceding chapter.

Water samples were collected between July 4th and July 28th 2004 and between July 7th and August 3rd 2005 and stored in polypropylene bottles at *in situ* temperature until experimental processing for photobleaching experiments, and at 20°C in an environmental chamber until microbial degradation experiments were carried out. The photobleaching experiments were performed *in situ* the day after water collection, whereas the microbial degradation assays started on August 20th in 2004 and on August 30th in 2005 in the laboratory (Quebec city) under controlled conditions. We used natural bacterial assemblages from each respective pond to inoculate the water.

Photobleaching protocol

Water was filtered through glass fiber filters (grade GF/F, MFS Advantec) to remove large particles (pre-filtered through 3 µm Nucleopore membranes in case of KWK2 to remove large plankton cells) and then through 0.2 µm sterile cellulose acetate filters at low pressure to remove most bacterial cells. Triplicate samples were irradiated with *in situ* natural sunlight using 1 liter clear Teflon bottles (BGR1: 78 h ; BGR5: 80 h ; KWK1: 98 h ; KWK2: 100 h ; BYL1: 327 h). The experiments occurred simultaneously in BGR1 and BGR5 (from July 10th to July 13th) and in KWK1 and KWK2 (from July 18th to July 21st). In the case of BYL1, the water was exposed to sunlight from July 30th to August 7th. Thus, the length of exposition was not the same for each bottle. Bottles were floating just under the surface of water. Duplicated control bottles (triplicate for BYL1) were covered with aluminium foil and wrapped in a black plastic bag. The bottles were subsampled at varying intervals depending on logistical constraints. Filtration through 0.2 µm membranes was done in the field and the samples were stored in the dark at 4°C for subsequent determination of DOM optical properties. Initial and final bacterial concentrations were also determined.

Microbial degradation protocol

2004 Experiments

The water was sampled on July 12th for KWK3 and July 21st for BON3, and kept at 4°C until filtered through 3 μm Nuclepore membranes on August 18th, at the beginning of the experiment. Live zooplanktons were observed in pond water at this date. Most of the volume of water was filtered through Vacucap 0.2 μm (Vacu 90) filters for BON4 and through 0.2 μm cellulose acetate filters for KWK3 and 250 mL was kept to prepared the bacterial inoculum by filtering 250 mL of the water through 0.8 μm Nucleopore filters. The water was subsampled for determination of initial conditions and the rest was used to filled four 300 mL BOD glass bottles; three of them were amended with the inoculum (1:9), the other bottle acted as a control. All the bottles were incubated at room temperature, in the dark, after stirring. The inoculated bottles were subsampled after 3, 12, 24, 45, 91 and 140 days for determination of the optical properties of DOM, the fourth one only at the final date.

2005 Experiments

The water was sampled at different moments in the summer of 2005; BGR1 : July 13th , BGR5 : July 13th, KWK1 : July 19th , KWK2 : July 19th , BYL1 : August 3rd. Water from the five ponds was filtered through 0.2 μm cellulose acetate filters at low pressure in the field just after the collection of samples (within 6 hours) and stored at 4°C in the dark. A natural bacterial inoculum prepared by filtration of at least 250 mL of the pond water through a 0.8 μm polycarbonate filter was stored at in situ temperature in the dark until the beginning of the experiment. Before starting the experiment, the filtered pond waters were subsampled to control for the concentration of bacteria grown during the 27-48 day delay period. The water was re-filtered through 0.2 μm cellulose acetate filters just before the beginning of the experiment to ensure that all bacteria were removed and amended with a solution of inorganic nutrients (equivalent to 0.1% of sample volume) to eliminate N and P limitation (5 μM $NaNO_3$, 5 μM NH_4Cl and 5 μM NaH_2PO_4 final concentration). We thereafter inoculated 1500 mL of the water with the natural bacteria inoculum (equivalent to 1% of sample volume) by concentrating 15 mL of the 0.8 μm filtered water on a 0.2 μm pore size polycarbonate filter and then resuspended in 15 mL of MilliQ water. Samples were taken to determine initial conditions (DOM and bacteria) and the water dispensed into fourteen 60-mL glass Teflon-capped bottles (treatment bottles). Ten additional bottles not inoculated (but with nutrient addition) served as controls.

Bottles were incubated in the dark in a controlled-environmental room maintained at 20°C. At each pre-determined sampling time (10, 19, 39, 80 and 140 days of incubation), triplicate treatment bottles and duplicate control bottles were taken (except for the last date when only two treatment bottles remained) for the determination of bacterial and DOC concentrations and DOM optical properties.

DOM characterization

See Material & Methods section of Chapter 2.

Bacterial count

See Material & Methods section of Chapter 2.

Results

General characterization of the ponds

Biology and chemistry

These ponds were part of a larger study on thermokarst ponds (**see Chapter 2**). **Table 9** summarizes the characteristics of the ponds, and **Figure 14** shows photographs of the ponds. The subarctic ponds (BGR1, BGR5, BON4, KWK1, KWK2 and KWK3) presented an essentially neutral or slightly acidic pH, while the water of the arctic pond (BYL1) was more alkaline. The ponds presented variable dissolved organic matter contents and total suspended solids (see below) and relatively high concentrations of nutrients as compared to other high latitude systems (average TP= 43.6 μg P L^{-1}, discussed in Chapter 2). The bacterial leucine incorporation rates measured in these ponds, as a proxy for bacterial production, indicate that thermokarst ponds are quite productive (ranging from 203 to 1195 pmol leu L^{-1} h^{-1}, for bacterial concentrations ranging from 1.7 to 3.2 $\times 10^6$ cells mL^{-1} in the 4 subarctic ponds sampled in 2005). The subarctic ponds were deeper than the arctic ponds, more stratified, with decreasing concentrations of oxygen and increasing concentrations of CO_2 and CH_4 with depth, the bottom waters often being hypoxic. **Table 6** shows surface and bottom water data for four ponds (BGR1, BGR5, KWK1, KWK2). It is important to note here that only surface waters were used for the transformation experiments. Refer to Chapter 2 for more information about correlations found between some properties and more discussion about general characterization of thermokarst ponds.

DOM characterization

A wide range of DOM concentrations and optical properties were represented within these seven ponds. For example, there were cases with both high DOC and CDOM (KWK1, KWK2, BON4), or both low DOC and CDOM (BGR1), the others being intermediate in either DOC, CDOM or absorptivity). BON4, KWK1 and KWK2 were the more "humic" ponds, while BYL1 also presented high DOC (9.4 mg L^{-1}) but lower absorptivity, BGR1, BGR5, KWK1 and KWK3 were more turbid compared to the other ponds, with TSS higher than 5 mg L^{-1} (and higher than their respective DOC contents), KWK1 being the least transparent pond (estimated Kd_{PAR} estimated from a model linking a_{320} and TSS yielded a value of 3.9 m^{-1}; **I. Laurion, pers. comm.**). BGR1 was the most transparent pond (estimated K_{dPAR} of 1.1 m^{-1}), with a deep turquoise color. The pond with the lowest spectral slope of CDOM absorption (S) is KWK3 (0.0133 nm^{-1}) and the pond with the highest slope is BYL1 (0.0163 nm^{-1}), the arctic pond.

The fluorescence of CDOM (such as measured with emission spectra for excitation at 370 nm; **Figure 6)** followed the same pattern as color (a_{320}), with three to seven-fold lower values in BGR1 and BGR5 than in KWK1, KWK2 and BYL1. The McKnight aromaticity indices (FI) calculated from the fluorescence emission spectra are shown in **Table 9**. These measurements are not available for the 2004 data. KWK1 and KWK2 presented the lowest indices, BGR5 and BYL1 intermediate values, and BGR1 the highest value. The maximum emission wavelength of fluorescence was lower in BGR1 compared to the other ponds (459 nm compared to a range of 464-467 for the others).

Figure 15 shows the synchronous-scan fluorescence (SF) spectra of all experimental ponds, featuring eight principal peaks (**emission wavelengths: 300(I), 362(II), 395(III), 416(IV), 439 (V), 487 (VI), 516(VII), 575(VIII) nm)** often accompanied with small shoulders at shorter and longer wavelength). The SF spectrum from BON4 differs from the others, with peaks being less distinct, lower fluorescence at shorter wavelengths, and higher fluorescence at longer wavelengths, i.e. a spectruim more typical of DOM from forested regions. The highest intensities of peak I were found in KWK1, KWK2 and BYL1, while peaks IV and V were highest in BGR5 and KWK1. Humification index calculated from these spectra are shown in **Table 9**. The values of HI for surface water were similar in BGR1, BGR5 and BYL1, but were slightly higher in KWK1 and KWK2.

Photobleaching experiments (only performed in 2005)

Results are shown in **Figures 16 to 19**. Decrease in DOC in BGR1,KWK1 and KWK2 were best explained by an exponential decay model (at rates of 0.06, 0.02 and 0.07 h^{-1}, respectively) and a linear decrease model in the two other ponds (BGR5: -0.006 and BYL1: -0.021 h^{-1}) (**Figure 16**; $P< 0.02$ except BYL1; results in percentage loss in **Table 8**). Decreases of a_{320} following exposure of surface water to natural sunlight seem to be explained by an exponential decay model in BGR1, BGR5, KWK1, KWK2 and BYL1 (**Figure 17**; percentage loss in **Table 10**). Photochemical loss rates of DOM color (a_{320}) are higher than for DOC in BGR1, BGR5, KWK1 and BYL1. In KWK2 loss rates of DOC were higher that loss rates of DOM color. Absorptivity generally tended to decrease in almost all ponds, except in KWK2 (**Figure 16**): BGR5 and KWK2 showed no clear tendencies, KWK1 showed a linear decrease in absorptivity, and an exponential decrease was observed in BGR1 and BYL1. Spectral slopes tended to increase exponentially with time in BGR5. In KWK1, KWK2 and BYL1, S increases exponentially with a rise to a maximum (plateau). A trend appears in BGR1, but no clear scheme is discernable (**Figure 17**).

Exposure to sunlight transformed the SF signal in all experiments. The fluorescence decreased at all wavelengths but in different proportions (**Figure 18;** means of replicates are shown). On an absolute scale unit, the major change in intensity was observed for peak IV, except in BYL1 where peak I was subject to the highest loss. On a relative basis, however, it appears that the highest losses of fluorescence were at the longest wavelengths. In KWK1, KWK2 and BYL1, the indices of humification decreased with time (**Figure 19** KWK1 and KWK2 are shown; linear regression, $P< 0.05$). In BGR1 and BGR5, there was no clear tendency.

Data from dark control bottles showed a clear trend of smaller changes compared to treatment bottles (difficult to determine percentages compared to the inoculated sample because standard deviations of TOC analyzer and the spectrophotometer were similar in magnitude to the difference between control and the treatment, but for DOC >90% remained compared to initial values and for a_{320} >94% remained compared to initial values), except in KWK2 where the changes were similar in control and treatment for DOC concentration, and BGR1 where a_{320} changed almost as much as in the treatment. Bacterial counts showed that there was a slight growth of bacteria in the control and treatment bottles during the experiments. The sterilisation by filtration was not complete; however bacterial numbers remained lower than 15% of in situ

natural concentrations, except in BGR1 where bacterial abundance was almost 100%. There was no correlation between bacteria growth and changes in the controls.

Microbial degradation experiments (2004 and 2005)

Bacterial counts showed that a re-growth had occured between water sampling and the beginning of the experiments in 2005 (from 0.22 to 1.18×10^6 cells mL^{-1}; 1-69% of *in situ*) even if the water had been filtered through 0.2 µm filters and kept at 4°C (data not available in 2004). A second count after the re-filtration previous to the inoculation showed that some bacteria remained in the water after filtration (from 0.03 to 0.34×10^6 cells mL^{-1}; 0.2-6% of *in situ*). There were as many bacteria in controls (non-inoculated bottles) as in the treatment bottles after 10 days of incubation (80-100% compared to treatment). Concentrations of bacteria diminished after this sampling at 10 days in control bottles. In inoculated bottle, bacterial counts during the course of the experiment showed an initial increase of cells in all ponds followed by a decrease (after 80 days in BGR5 and BYL1, and after 19 days in KWK1 and KWK2) and an increase again at the end. BGR1 is the only case where bacteria did not decline during the experiment. Since bacterial counts in non-inoculated bottles showed significant growth of bacteria at the beginning of the experiment, these can not be used as controls.

2004 experiments

Results are shown in **Figures 20** and **21.** The two ponds experienced an exponential decrease in DOC concentrations (at rates of 0.006 d^{-1} in BON4 and 0.041 d^{-1} in KUJ3; $P< 0.005$) and in CDOM absorption coefficients (at rates of -0.026 in a linear decrease for BON4 and 0.007 d^{-1} in an exponential decay in KUJ3; $P< 0.01$), but since decreases in absorption were slower than declines in DOC, there was a significant logarithmic increase in absorptivity with time (at rates of 0.036 d^{-1} in BON4 and 0.030 d^{-1} in KUJ3; $P< 0.03$). Spectral slopes tended to decrease with time in KUJ3, whereas they tended to increase in BON4.

2005 experiments

Results are shown in **Figure 22** to **25**. Decreases in DOC were best explained by an exponential decay model in all ponds (**Figure 22**; rates varied between 0.024 to 0.067 d^{-1}, being maximal in pond KWK2; **$P< 0.02$**). Absorptivity significantly increased in KWK1 (at an exponential rise of 0.013 d^{-1}; **$P< 0.0001$**) and decreased in KWK2 and BYL1 (with an exponential rate of 0.012 and

0.145 d^{-1}, respectively; P< 0.0001) (**Figure 22**). There were no significant trends in BGR1 and BGR5 in absorptivity, nor any trends in changes of spectral slopes in all ponds (**Figure 23**). Decreases CDOM absorption measured at 320 nm (a_{320}) with time were best explained by an exponential decay model (**Figure 23**; rates ranging between 0.016 and 0.065 d^{-1}, being maximal in KWK1; P< 0.0002), except in BGR1 where there was no clear trend.

Microbial degradation transformed the fluorescence signature of DOM. The fluorescence decreased at all wavelengths but in different proportions. In all five ponds, the loss of fluorescence intensity was higher at the shortest wavelengths on an absolute scale (**Figure 24).** On a relative scale there was no clear trend, except in BYL1 where molecules fluorescing at the shortest wavelengths were clearly more affected. The two indices of humification tended to increase with time (P= 0.10), except in BGR1 where there was no clear trend (**Figure 25**).

Data from dark control bottles showed changes in many DOM characteristics (a_{320}, DOC, S) in all ponds, except BGR1, in the first ten days. However, DOC remained more stable thereafter (> 10 d) in the incubation, in all ponds. The different characteristics changed up to 100% (>90%) compared to treatment bottles after 10 days. Hence, because of the bias found in the first days of the incubation, non-inoculated bottles cannot be used as controls for microbial degradation.

Discussion

Thermokarst ponds are productive ecosystems, with relatively high concentrations of nutrients and abundant microbial communities. They contrast with the oligotrophic status generally observed in aquatic systems at high latitudes. Intuitively, we can suspect these productive systems to have a notable impact on the mobilization of the carbon stocked in the soils for thousands of years. High latitudes are particularly sensitive to climate changes and contain a large pool of carbon (see Chapters 1 and 2). Several models have been developed to assess the future effects of climate changes on these fragile ecosystems and on global carbon cycling (e.g., **Lawrence and Slater 2005 and references therein**). Unfortunately, field data to assess the transformations of the organic matter in high latitude ecosystems are scarce, and present biogeochemical models are not representative enough of the conditions prevailing at these latitudes (**Hobbie et al. 2000).** The contribution of DOM to global carbon budgets, including responsiveness to climate changes, is only beginning to be addressed (**Findlay & Sinsabaugh 2003**).

The decomposition of a large pool of DOC could lead both directly (by photolysis of organic matter) and indirectly (via microbial respiration) to an increased release of greenhouse gases. Our experimental results address 1) the potential role of photochemical processes in controlling the residence time of DOM in thermokarst ponds, and 2) the influence of aquatic microbial communities on the cycling of DOM.

General characterization of the ponds

Physical and environmental variables

The ponds chosen to perform the experiments presented a range of optical properties represented by their content in DOM and TSS and perceptible from their apparent color. This variability was also reflected in other limnological characteristics, such as vertical structure, pH, nutrients, dissolved gases, microbial biomass and productivity (see Chapter 2 for details). All ponds were of small area and volume, and they were all stratified (profiles only available in 2005) except for BYL1, but this latter was quite shallow (z_{max}= 0.6 m; although other shallow ponds at Bylot were stratified).

Concentrations of dissolved CO_2 and CH_4 showed considerable variation among ponds and between depths. The highest concentrations were found at the forest-tundra site (Boniface River), and all ponds except BYL1 were oversaturated compared to the atmosphere. Other ponds similar to BYL1 (i.e., formed over a depressed polygon, as opposed to melted ice wedges where oversaturation was found) were similarly found to be in the same state of saturation relative to the atmosphere. They are more exposed habitats often sheltering rich microbial mats (**Vézina and Vincent 1997**) that surely affect this gas equilibrium. This oversaturation in both CO_2 and CH_4, in addition to the relatively high phosphorus concentrations, are indicative of a productive environment. Bacterial abundance and productivity were indeed high in the ponds. On the other hand, the Chl *a* concentrations ranged from 0.4 to 3.7 $\mu g\ L^{-1}$, indicative of oligotrophy. This result could be explained by the low transparency of water to sunlight or by the high abundance of zooplankton observed as explained in Chapter 2.

DOM Characterization

Two of the lowest DOC values were found in ponds originating from shrub tundra (BGR) where the vegetation was less extensive compared to the forest tundra (BON). However, the highest DOC value was observed in the arctic pond where trees and shrubs were absent, but vegetation

was highly abundant and dominated by sedges (see Study sites). The ponds also presented varying CDOM concentrations. In the case of BYL1, an intermediate value of CDOM was associated with a relatively low value of absorptivity. BYL1, the arctic pond, experienced continual exposure to sunlight in summer (i.e., uninterrupted photobleaching).

The spectral slope gives information regarding DOM composition. It is generally accepted that high S values in the UV-visible region are associated with microbially-derived or highly degraded DOM, while lower slope values are more typical of terrestrially-derived DOM or less diagenetically altered material (see reviews by **Markager and Vincent 2000**; **Twardowsky et al. 2004**). The relatively low slope values found in the studied ponds indicate a typical terrestrially-derived DOM, the higher slope of BYL1 indicating either a contribution from microbial mats or more degraded DOM (in situ photobleaching or long term diagenetically altered peat soils). The determination of the fluorescence index from emission scans (FI) also gave indications on the quality of DOM at the beginning of the experiments (**McKnight et al. 2001**). Values confirmed the terrestrial origin of DOM for BGR5, KWK1, KWK2 and BYL1. The FI value of BGR1 (1.34 or a corrected value of 1.62; see Chapter 2 for details) indicates both microbially and terrestrially derived organic material contributing to DOM (**McKnight et al. 2001**). However, there were no apparent microbial mats or macrophytes, nor was there a high phytoplankton biomass in this pond. However, it is possible that benthic microbial assemblages out of sight may have contributed to the DOM pool.

The ponds sampled in 2005 were characterized by similar synchronous-scan emission spectra featuring eight principal peaks designated I to VIII and classified in three categories of molecular weight (for more details see chapter 2), but the relative contribution of each fluorophore was not the same. The most striking difference was found in BON4 with a high contribution of HMW components. Also the relative contribution of peak I was higher in the KWK ponds and BYL1, indicating that the contribution of amino acid/protein-like component, presumably more easily assimilable (e.g. largely consumed in experiments with different phylogenetic groups; Cottrell and **Kirchman 2000**) was higher in these 3 ponds. According to these spectra, BON4 presented the most complex assemblage and had the lowest contribution of the protein-like component. Finally, the index of humification calculated from the SF spectra revealed a similar degree of humification in ponds BGR1, KWK1, KWK2 and BYL1. BGR5 presented a slighly lower degree of humification. Absolute values of these indices cannot be directly compared with results from studies using another instrument since measurements were not corrected with standards (**Kalbitz**

and Geyer 2001). However, these values resemble what was found in water sampled from intact peatlands (**Kalbitz et al. 1999**). The different age of the ponds and hence of the mobilized carbon dissolved in them possibly affect this humification index.

Photochemical degradation

The absorption of light by DOM results, in the modification of its light-absorbing capabilities and the formation of photoproducts. Among these photoproducts are inorganic compounds (e.g., carbon dioxide and monoxide) that generally have no effect on the microbial food web (**Moran and Covert 2003**). However, photochemical mineralization has impacts on gas transfer at the water-atmosphere interface. In addition, some compounds resulting from photolysis are directly available (labile) for heterotrophic bacteria (e.g., low molecular weight carboxylic acids like pyruvate; **Kieber et al. 1989, Bertilsson and Tranvik 2000**). Our results provide evidence that a significant fraction of the DOM pool in thermokarst ponds can be photodegraded (5-14% of DOC; 13-36% of CDOM; **Figure 16** and **Table 10**) during short-term exposure to natural sunlight. DOC losses of over time and qualitative change in the different spectroscopic signatures of the water were observed. In fact, relatively important and significant losses of DOC were observed in all ponds, but the kinetic varied between ponds. These losses calculated for thermokarst ponds are not surprising since photochemical processes have been previously identified as an important mechanism for the degradation of terrestrial DOM (e.g. **Kieber et al. 1989**; **Miller and Zepp 1995**; **Amon and Benner 1996**; **Graneli et al. 1996**; **Opsahl and Benner 1998**; **Moran et al. 2000**; **Obernosterer and Benner 2004**). The exponential decrease of DOC in the KWK ponds and BGR1 indicates the presence of DOM more reactive to photolysis as compared to BGR5 and BYL1 which showed a linear decrease in DOC.

Granéli et al. (1996) estimated photo-oxidation rates from the production of DIC at different depths in five Swedish lakes (similar latitudes as our ponds). Water was incubated in quartz tubes from sunrise to sunset (approximately 18 hours of natural light), after which DIC was measured manually. They estimated DIC production to range between 86 to 410 mg C m^{-3} d^{-1} at the surface. We did not follow DIC in our experiments, but the decrease in DOC can be interpreted as an indirect estimation of inorganic carbon production if we consider that the fraction incorporated into microbial biomass in the short term is insignificant. For example, the quantity of DOC lost over twenty seven hours in BGR1 was 0.33 mg C L^{-1}. These rates were calculated using the second sampling point, always after more than 24 hours, to account for the different light doses

received over 24 hours. The rate of mineralization for a complete day can then be estimated to be 0.29 mg C L^{-1}. This corresponds approximately to a mineralization rate of 290 mg C m^{-3} d^{-1}. The same calculation was done for the other ponds (**Table 10**). Our estimated rates of photo-oxidation are then comparable to the observations for Sweden humic freshwaters. However, DIC is also produced by microbial respiration and DOM photolysis can produce other compounds than DIC. Change in CDOM absorption and fluorescence properties provides complementary information about on the photolytic transformation of DOM into other organic compounds.

During our photobleaching experiments, CDOM (a_{320}) and absorptivity tended to decrease with time of exposure, whereas the slope S increased in most cases, as in other lake systems (**e.g. Twardowski and Donaghay 2002**). CDOM (**Table 10:** 14-36%) was more affected by photobleaching than bulk DOC (**Table 10:** 5-14%), with different kinetics of change among ponds. DOC mineralization rates indicated that KWK2 had the most photoreactive DOM, followed by BGR1, KWK1, BYL1 and BGR5. CDOM (a_{320}) loss rates followed essentially the same order except that BYL1 presented a net change in a_{320} while the change in DOC was minor (see below). The radiation dose was different among sites (only ponds from the same site were exposed simultaneously). Thus, the day length cannot be control for. In particular, BYL1 was exposed to 24 h sunlight in July, with the shallower depth and a unique light history. This was reflected in the initial pool of DOM, as shown in SF spectra, particularly for HI-1, which was lower than in the other ponds. In fact, the initial DOM characteristics (note that they are slightly different from data in **Table 9** since there was a delay between sampling and experiments) showed a higher degree of polycondensation and humification (HI-1, **Figure 17**) in BGR ponds (BGR1=0.81; BGR5=0.82), followed by KWK ponds (KWK1=0.78; KWK2=0.79) and the high arctic pond (BYL1=0.73) (not enough data for statistical analysis). This is where the difference between subarctic and arctic ponds is most perceptible (more so far for the overall SF spectra). It seems that there are less complex molecules in BYL1. The incessant photobleaching at this time of year probably explains this difference and why a_{320} loss was less extensive in this pond.

In all of our studied ponds, exposure to sunlight decreased the overall fluorescence signal (such as in **Pullin and Cabaniss 1997** for example). In all ponds, higher percentages of fluorescence losses were found at the longest wavelengths (**Figure 18**), which can be attributed to losses of more complex, HMW terrestrially-derived substances. On the other hand, there is a clear reduction in the region of peak I in **Figure 18.** This small decrease in fluorescence could be at least partly attributed to the presence of bacteria in the incubation bottles (bacterial growth was

measured in dark control bottles even though the water was pre-filtered; see Discussion in Chapter 2). Since there was no important change in DOC or a_{320} in control bottles in most of the ponds, it seems that regrowth of bacteria did not cause a problem in the experiment. The photobleaching was a short term experiment and thus microbial regrowth was unlikely to causebiases.

At the end of the exposure period to sunlight, there were no particular changes of the indices of humification (HI) in BGR1 and BGR5, while they tend to decrease with time in KWK1, KWK2 and BYL1 (**Figure 19**). This may reflect a decreasing aromatic content of fulvic acid after exposure to sunlight in these three ponds. Lower absorptivity values and humification indices have been linked to a higher percentage of DOC mineralization through biodegradation **(Kalbitz et al. 2003)**. The decrease in HI in our own experiment may indicate that exposure to sunlight increased the lability of DOM for further microbial degradation, at least in KWK1, KWK2 and BYL1. Our results showed that photobleaching decreased the complexity of DOM (HI, absorptivity, slope). This should benefit microbial degradation, since complex HMW DOM is expected to be more resistant to biological degradation, being older and more aromatic. DOM in thermokarst ponds is predominantly terrestrial and showed the potential to be transformed by photobleaching. Recent studies have shown that terrestrially derived DOM will generally have enhanced lability following irradiation (**Moran and Covert 2003 and refs therein**). Without direct measurements, it is difficult to estimate if DOM photolysis in thermokarst ponds changed the lability of organic matter. An experimental set-up including measures of microbial degradation following photobleaching would be of interest (e.g. **Amon and Benner 1996**; **Moran et al. 2000**; **Obernosterer and Benner 2004**). In addition, an experimental setup with airtight compartments would allow the measurements of gas production and direct quantification of DOM mineralization through photolysis.

It is important to note that many thermokarst ponds (and the 5 subarctic ponds studied here) presented high inorganic turbidity (clay particles less than 2 μm and silts between 2 and 50 μm, see **Chapter 2, Table 4**). To perform photobleaching experiments, we needed to remove biotic particles through filtration (>0.2 μm), i.e. that is, most of suspended material, including inorganic particles. **Tietjen et al. (2005)** showed that the presence of suspended clay increased photochemical decomposition of CDOM. This was explained by clay-induced light scattering. Such scattering increased scalar photon flux density (or fluence rate) under the experimental conditions representing the surface water. **Tietjen et al. (2005)** suggested that solar radiation can

directly decompose adsorbed organic matter and facilitate desorption of it. Hence, the photochemical degradation rates that we measured in thermokarst ponds may be underestimated. More studies are needed to assess the extent of this affirmation.

Overall, although the experiments performed in the present study do not exactly represent the reactivity of DOM under natural conditions (experiments were performed in a closed system and Teflon bottles slightly reduce light), they revealed the difference in the response of the DOM pool among thermokarst ponds, when exposed to natural sunlight.

Microbial degradation

Given the central role of DOM in the microbial food web, there is broad interest in measuring and comparing the bioreactivity of DOM from different sources (**Benner 2003**). Only a minor fraction of DOM is directly available for utilization by heterotrophic microorganisms (**Sondergaard et Middelboe 1995**). There are alternative mechanisms that render the organic material less refractory and thereby facilitate bacterial utilization of this energy source, such as the use of extracellular enzymes (**Arnosti 2003**) and photochemical-mediated processes (**Moran and Covert 2003**). In the present study, we measured the degradation of DOM in thermokarst ponds by incubating filtered water with natural microbial communities in the dark for 140 days. Contrary to the phototransformation experiments, the incubations were performed under controlled conditions that were the same for all ponds.

Our results provide evidence that a significant fraction of the DOM pool in thermokarst ponds can be biologically degraded. We observed significant losses in organic matter over 140 days (**Table 11:** 14-30% bulk DOC; 9-42% CDOM) and qualitative changes in DOM pool (**Figure 22 to 25**). A higher percentage of DOC was lost after 140 days in 2005 (21-30%) compared to the 2004 experiments (14-22%). The kinetics of change in optical properties reflect the DOM reactivity in the presence of natural bacterial assemblages. In thermokarst ponds, we only observed exponential decreases in bulk DOC with time. Linear kinetics are indicative of the absence of a significant reservoir of labile and rapidly cycling DOC (**Moran et al. 2000**). Thus, despite the delay between sampling and start of the experiments, and the growth of bacteria during this period, it seems that some rapidly cycling DOM was present in the water (or some was produced in the bottle prior to the incubation) at the beginning of the experiments in 2005.

Long-term decomposition of DOM in waters of different origin was studied by **Obernosterer and Benner (2004)**. The incubation time needed until no change in DOC concentration was observed (plateau) reached 111 to 297 days in lake and swamp waters. Up to 27% of DOC was removed by bacteria from these waters. In our experiments (all except BON4), the incubation period was sufficient to reach this plateau since the differences in DOC concentration between the two last sampling points fall within the instrumental deviation. We can then hypothesize that no further change would have happen later on, reflecting a reservoir of labile DOM (21-30% DOC subject to microbial degradation) comparable to that obtained by **Obernosterer and Benner (2004)**. However, the time needed for microbial assemblages to use all of the labile DOM was shorter ($\leq$ 80 d). In BON4, the incubation period was not long enough to reach this plateau, reflecting the more recalcitrant nature of the DOM in the forest tundra. **Søndergaard and Middelboe (1995)** summarized the results of 126 measurements of bacterial degradation using a similar approach. The concentration of labile DOC (DOC_L), defined as the amount of DOC that can be decomposed within a week or two, was determined. In this review, DOC_L expressed as a percentage of total DOC was found to be 14 ± 8% in lakes, 19 ± 16% in rivers, and 19 ± 12% in marine waters. We estimated DOC_L in our experiments by computing the remaining DOC after 14 days of incubation. DOC_L varied between 2 and 13% (**Table 11**) which is comparable to the literature for lakes.

We cannot directly compare results between 2004 and 2005 because the experimental set-ups were different. In 2004, the water was filtered only at the moment of the beginning of the experience. Then, the grazers (live zooplankton described at the beginning of M & M section) continue to feed on bacteria until the beginning of the degradation experience (approximately 4 weeks). Also, because of the presence of these grazers, there was a constant input of autochtonous DOM. However, it is impossible to quantify this input. The question remains: Is the input of new DOM compensating in some way the grazing of bacterioplankton? We think that the method used in 2005 was better able to quantify the real microbial degradation because it did not introduce such a bias. However, as this paper is of the first to consider microbial degradation in thermokarst pond in particular, we decided to provide as much data as possible. Thus, the particularities of each experiment should not be forgotten when inferring microbial degradation processes in thermokarst ponds. In 2005, the experiments began up to 6 weeks after sampling (e.g., BGR ponds), leaving time for microbial utilization of the most labile DOM. In 2004, the bacteria were not removed immediately after sampling, and in 2005, re-growth (up to 69% of the in situ concentration) occurred even though the pond waters were pre-filtered shortly after sampling. In

study of environments such as thermokarst ponds, unfortunately, many logistical constraints must be taken into account. The delay in storage caused by transport, which brings storage artefacts, bacterial growth, chemical change, etc., is unavoidable.

In the 2004 experiments, the two ponds gave very different results. The loss rate and the percentage of DOC lost were much lower in BON4 (0.006 day^{-1}, 14% total DOC loss) than in KWK3 (0.041 day^{-1}, 21% total DOC loss). This is not surprising since these two ponds presented initially large differences in their DOM composition (revealed by their synchronous fluorescence spectra in **Figure 15**). BON4 is located in the forest tundra, where larger molecules are likely more abundant (probably in large part lignin and its derivatives; large peaks at longer wavelengths in its SF spectra were associated with the presence of peat in Chapter 2) and presumably less labile. In addition, the increasing absorptivity during the incubation period likely occurred because non-chromophoric DOM was preferably assimilated by bacteria. In the 2005 experiments, loss rates of bulk DOC were generally of the same magnitude (0.024-0.067 day^{-1}) but higher loss rates were found in two of the three ponds having a higher peak I, which is known for its lability (**Figure 15 b**). In addition, changes in CDOM relative concentration (a_{CDOM}/DOC) did not follow a consistent trend (decrease in the KWK2 and BYL1 samples, increase in the KWK1 sample, no trends for the BGR samples). These differences probably reflect diverse DOM compositions and microbial assemblages in these optically and limnologically distinct environments. The initial DOM pool certainly has an impact on microbial degradation rates.

Synchronous fluorescence scans clearly showed that the relative loss of fluorescence intensity was highest at the fluorescence spectrum extremes (**Figure 24**). However, fluorescence was lower at longer wavelengths and hence it is easy to reach large relative changes. On an absolute scale, the highest losses were found at the shortest wavelengths, especially in BYL1. The lowest relative loss of fluorescence was situated around 420-470 nm (emission wavelength) in the BGR1, BGR5, KWK1, and KWK2 incubations. This range was rather 445-495 nm in the BYL1 sample. This may be indicative of the molecular sizes preferentially decomposed by bacteria. These differences are not surprising since the arctic pond is really distant from the others, with more chances of having a unique microbial community acclimated to the environmental conditions prevailing there.

These synchronous fluorescence scan results showed that bacteria in thermokarst ponds can degrade a relatively large range of DOM molecules, without the contribution of photobleaching.

In the literature, molecular weight or size is often mentioned as an important factor influencing the microbial utilization of DOM. **Saunders (1976)** formulated the general model that simple molecules decompose quickly, within hours. Phytoplankton-derived HMW organic compounds decompose within days to weeks, while other HMW compounds decompose over time period on the order of months or more. Although this conceptual model is still widely accepted, other studies indicate that some HMW compounds are rapidly used by bacteria (**e.g. Tranvik 1990; Arnosti et al. 1994**). The first sampling point of our experiment occurred after 10 days of incubation so we cannot evaluate the importance of rapidly cycling DOM, but at this time the loss of fluorescence intensity was already evident in the range 250-550 nm for the five ponds. Heterotrophic bacteria are faced with the fundamental challenge of obtaining sufficient carbon and energy from the organic substrates in their environment (**Arnosti 2003**). Many LMW substrates can be transported into the cell, across cytoplasmic membranes in an enzymatic process involving permeases. Higher molecular weight DOM however must be hydrolyzed outside the cell to sizes small enough to permit transport across the outer membrane (**Wetzel 2001**). Extracellular enzymes are therefore required to initiate the remineralization of HMW organic matter (**Arnosti 2003**). The utilization of the HMW component by bacteria is likely explained by the presence of such enzymes in the thermokarst pond microbial communities. The arctic pond community clearly showed a lower extent of degradation of HMW molecules. Such enzymes may be absent or in lower quantity in arctic ponds, or enzymes are present but the colder temperature of the water suppresses their activity. It is important to note however that the experiments were all performed at 20°C, which is higher than the in situ temperature of BYL1 but similar to the temperatures of subarctic ponds in July. The HI index, an estimation of the degree of humification and polycondensation in the DOM pool, increased with time during the incubation (**Figure 25**). This result suggests a preferential uptake of less complex molecules by bacteria in our experiments. **Kalbitz et al. (2003)** showed that solutions exceeding a threshold value of UV absorbance, aromaticity or humification indices derived from fluorescence spectra were relatively stable against biodegradation.

As there was a slight growth of bacteria in the media before the beginning of the experiment, a non-negligible fraction of DOM could have already been used by bacteria when the experiments started. For that reason, our DOM loss rates can be considered conservative. In addition, since the inoculum was filtered through 0.8 μm, we artificially selected for smaller bacteria. Likewise, since the media were filtered through 0.2 μm filters, we removed particulate carbon and the particle-associated bacteria. Bacteria can obtain DOM through enzymatic degradation of

particulate organic matter (**Wetzel 2001**) and previous studies showed that a large fraction of the bacterial production is associated with these bacterial communities in thermokarst ponds (see Chapter 2; $\geq$ 82%). Further determination of the potential of these communities to use dissolved material is an interesting and challenging avenue for future investigations of DOM reactivity. Long-term incubation in a closed system with new environmental conditions certainly changed the natural bacterial assemblages and the contribution of each species to the overall DOM degradation processes. Despite some shortcomings, this type of bioassays remains the best approach for estimating the bioavailability of DOM (**Benner 2003**). Our experiments helped us to estimate the microbial contribution to the degradation of DOM pool liberated in thermokarst ponds by the melting of permafrost, and to compare this to photochemical processes.

We have shown in Chapter 2 how thermokarst ponds present a wide array of limnetic conditions. They are not a static system with a clear predicable response to DOM degradation processes. A larger number of ponds would need to be assessed under more natural conditions to determine the precise contribution of microbes to the turnover of DOM. Extrapolation must be done carefully since significant differences have been found in ponds in close proximity. In addition, temporal variations in microbial degradation rates have been observed in the literature (e.g., up to 13-fold in an estuary, **Moran et al. 1999**). Therefore, quantitative interpretation of the measured loss rates should be used with caution.

Comparison of the two degradation processes and perspectives

Theoretically, DOM in thermokarst ponds can have several autochtonous and allochtonous origins: microbial exudates, decomposition of recently submerged terrestrial vegetation, peat soil from melting permafrost, etc. Our general characterization of DOM, using the fluorescence index of **McKnight et al. (2001)**, allowed us to determine that the predominant source of DOM in thermokarst ponds is terrestrial, with a significant content of aromatic carbon, although there are indications that autochtonous inputs were not negligible. DOM with this terrestrial signature is likely coming from the plants in the drainage basin (presumably very small, given the unique topography of this environment, at least in the case of subarctic ponds) and partly decomposed organic matter stocked in permafrost. Renewal time of pond water is presumably long and is determined by the precipitation and evaporation regimes since there are no inlets/outlets. To further study the contribution of each source, an extensive study including the determination of isotopic ratios ($\delta^{13}C$ and $\delta\ ^{15}N$ signatures of carbon and nitrogen in water are conservative and

representative of the ratios present in plant and organic soil from which they originate) would be useful. Of particular interest is the newly mobilized organic matter from melted permafrost, because it represents a new source of carbon previously stocked in soils for hundreds or thousands of years, which has not been taken into account in most climate models.

Rates of photochemical and microbial DOM degradation calculated in thermokarst ponds are presented on the same scale for the purpose of comparison between the two degradation processes (**Table 12**). Although we are comparing different experimental conditions (*in situ* versus controlled) and time scales (short-term versus long-term), the results shows that photochemical degradation is a much faster DOM mineralization process than is microbial degradation (from 6 to 26 times). The higher effectiveness of photolysis compared to microbial degradation in organic carbon mineralization has been demonstrated in other systems. In surface ocean waters, based on observed DIC formation rates, **Miller and Zepp (1995)** showed that photooxidation of DOC by sunlight should be considered a dominant removal mechanism for organic carbon. **Amon and Benner (1996)** also measured higher rates of DOC photolysis in the Amazon River system (sevenfold greater than bacterial DOC utilization). However, in this latter study, integrated over the entire water column, microbial remineralization was the dominant process for oxygen and DOC consumption.

In the stratified and turbid thermokarst ponds, DOM in the bottom waters is "protected" from sunlight but may become exposed repeatedly for sustained periods of time during seasonal mixing events (**Imberger 1995**; **Wetzel 2001** and Chapter 2). The work of **Biddanda and Cotner (2003)** showed that water with little recent exposure to sunlight experienced increased bacterial degradation rates after exposure to sunlight. Therefore, photochemical alterations in sunlit surface waters appear as a unique mechanism for the turnover of carbon in aphotic environments (**Benner and Biddanda 1998**; **Anderson and Williams 1999; Biddanda and Cotner 2003**). These mixing periods could have a significant impact on the turnover of DOM by generating highly labile DOM for further microbial degradation. The quantity and quality of DOM is then a key factor, in combination with factors that affect the vertical structure of the water column (temperature, turbidity etc.), that will influence carbon fluxes from thermokarst ponds to the aquatic ecosystem and the atmosphere. For example, if temperature continues to rise in Polar regions, decomposition rates (and greenhouse gas fluxes) may increase due to an extended ice-free season and warmer water temperatures, but only if DOM is available for microbial degradation.

Due to their presence at high latitude, thermokarst ponds experience elongated sunlight exposure for photobleaching during the ice-free season, in combination with an abundant microbial community actively respiring the available carbon. On the other hand, increased growth of plants and trees could compensate for these new sources of greenhouse gases, and the system could eventually become a net sink for atmospheric CO_2. The question is: which of these processes (decomposition versus primary production) will dominate? The present work (in combination with Chapter 2) is a first step towards understand the complex processes that could lead to this potentially massive release of greenhouse gases. If DOM is recalcitrant, it will not interfere with any processes, but may possibly adsorb to clay particles and sediment or stay in the water until the pond is drained or recolonized by aquatic plants. Part of the DOM may eventually be transported to the ocean via the drainage basin (**Benner et al. 2004**), although it is unknown if this will represent a significant input of organic matter to the ocean. Increasing inputs of DOM to the coastal ocean certainly would influence thermal and light regimes, which control several microbial food web processes. On the other hand, reactive DOM will be mineralized into inorganic compounds or transformed into other organic components. In both cases, transformations of DOM will eventually lead to the release of CO_2 or CH_4 if there is no colonization by plants or drainage of the pond. Due to a combination of ongoing changes in temperature and precipitation, the dynamics of DOM in high latitude aquatic ecosystems will certainly change.

Figure 14 : Photographs of the ponds sampled for DOM degradation experiments in 2005
a. BGR1, **b.**BGR5, **c.** KWK1, **d.** KWK2, and 2004 **e.** BYL1, **f.** KUJ3, **g.** BON4

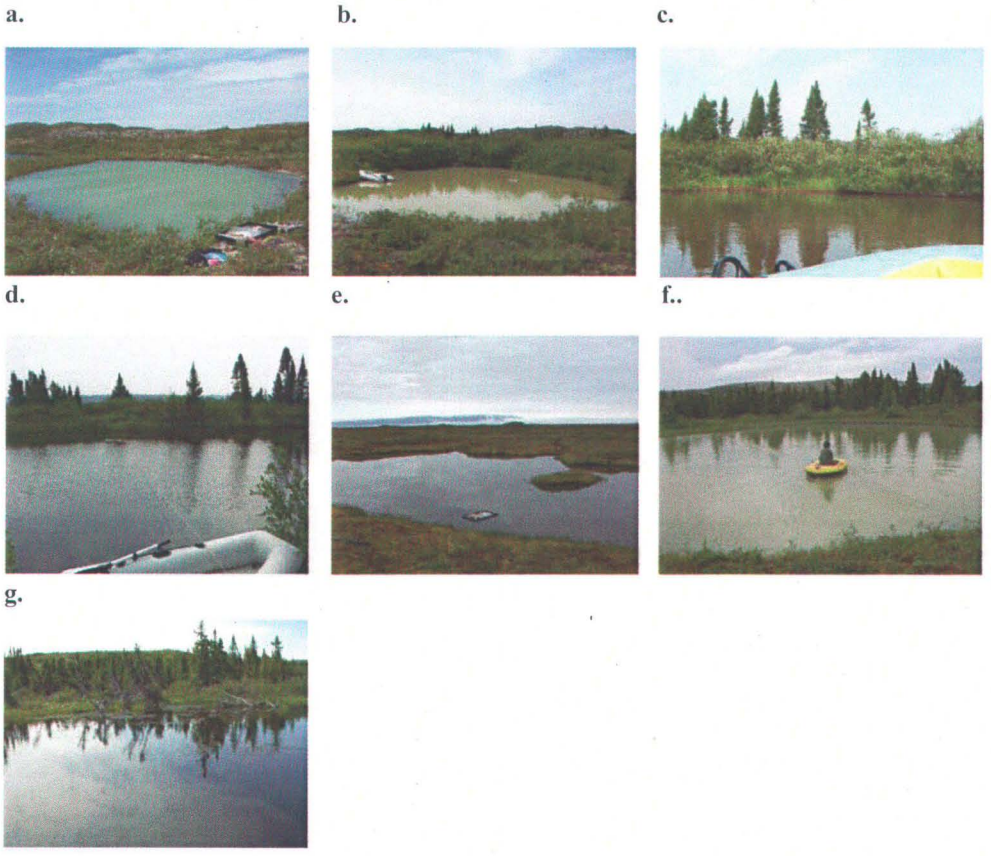
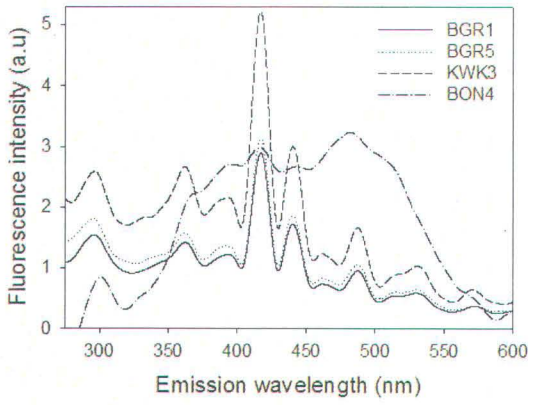


Figure 15 : Synchronous fluorescence spectra of DOM from pond waters studied in the 2004 and 2005 experiments

a. Ponds BGR1, BGR5, KWK3 and BON4. b. Ponds KWK2, BYL1 and KWK1.

Note the higher contribution of longer wavelength fluorescence in BON4 Spectra are regrouped according to similarities in their peak relative contribution and intensities, particularly by the relative importance of their peak I.

a.



b.

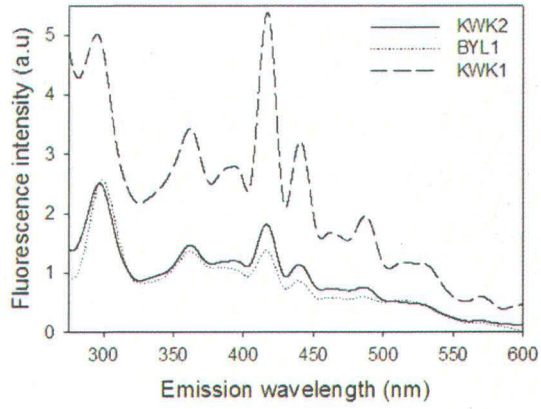


Figure 16: Changes in DOC concentration (black circles, solid line) and absorptivity (gray squares, dotted line) during DOM photobleaching experiments in 2005

in **a.** BGR1, **b.** BGR5, **c.** KWK1, **d.** KWK2 and **e.** BYL1. Mean values of triplicates and standard devation, and r^2, P value and k (slope of curve, exponential or linear, in $hour^{-1}$) of fitted curve (when available) are shown (DOC regression parameters in black; absorptivity regression parameters in gray). Note that time scale varies.

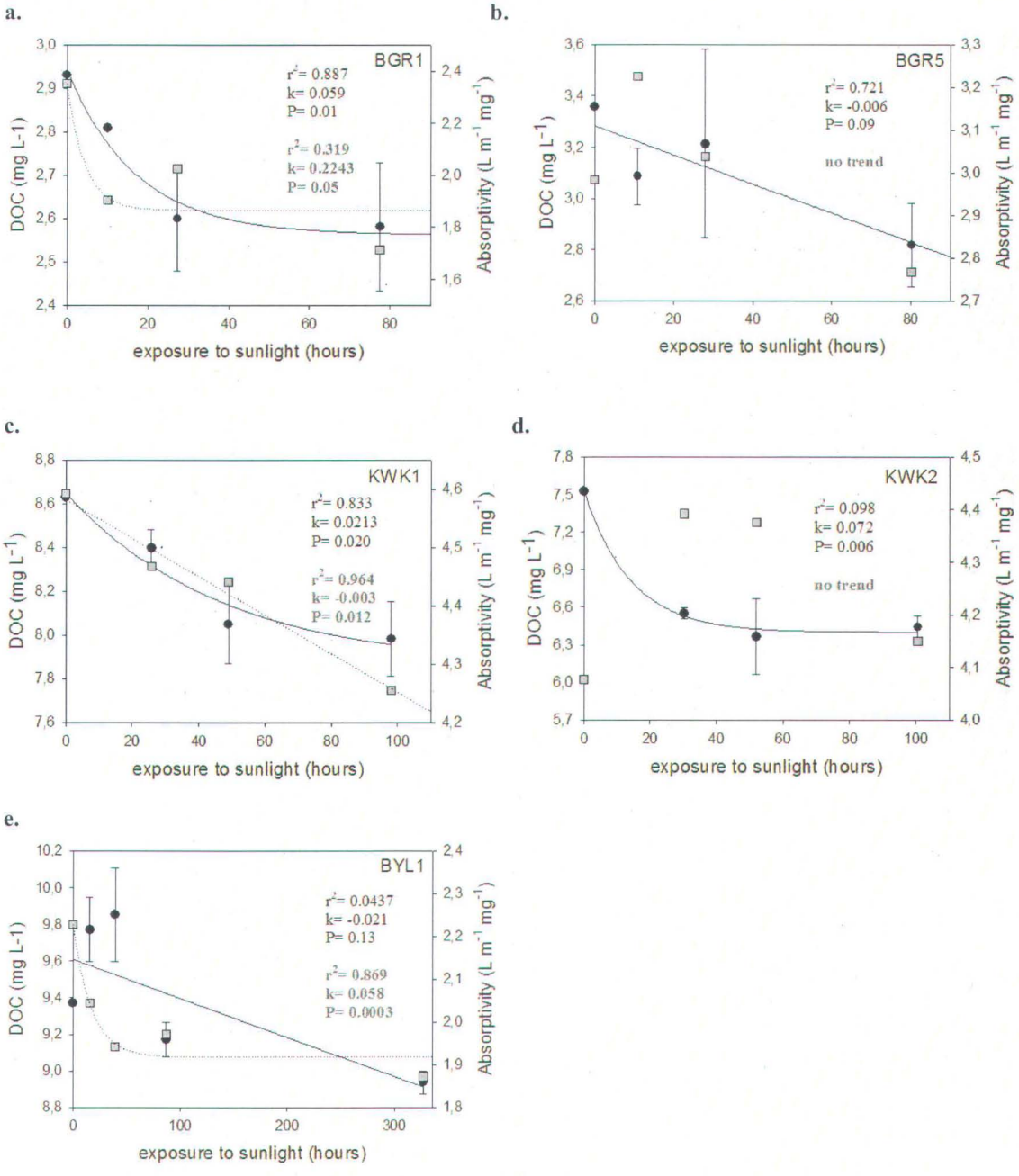


Figure 17: Changes in CDOM a_{320} (black circle, solid line) and spectral slope (gray squares, dotted line) during DOM photobleaching experiments in 2005

in **a.** BGR1, **b.** BGR5, **c.** KWK1, **d.** KWK2 and **e.** BYL1. Mean values of triplicates and r^2, P value and k (slope of curve, exponential or linear, in $hour^{-1}$) of fitted curve (when available) are shown. (a_{320} regression parameters in black; spectral slope (S) regression parameters in gray). Note that time scale varies.

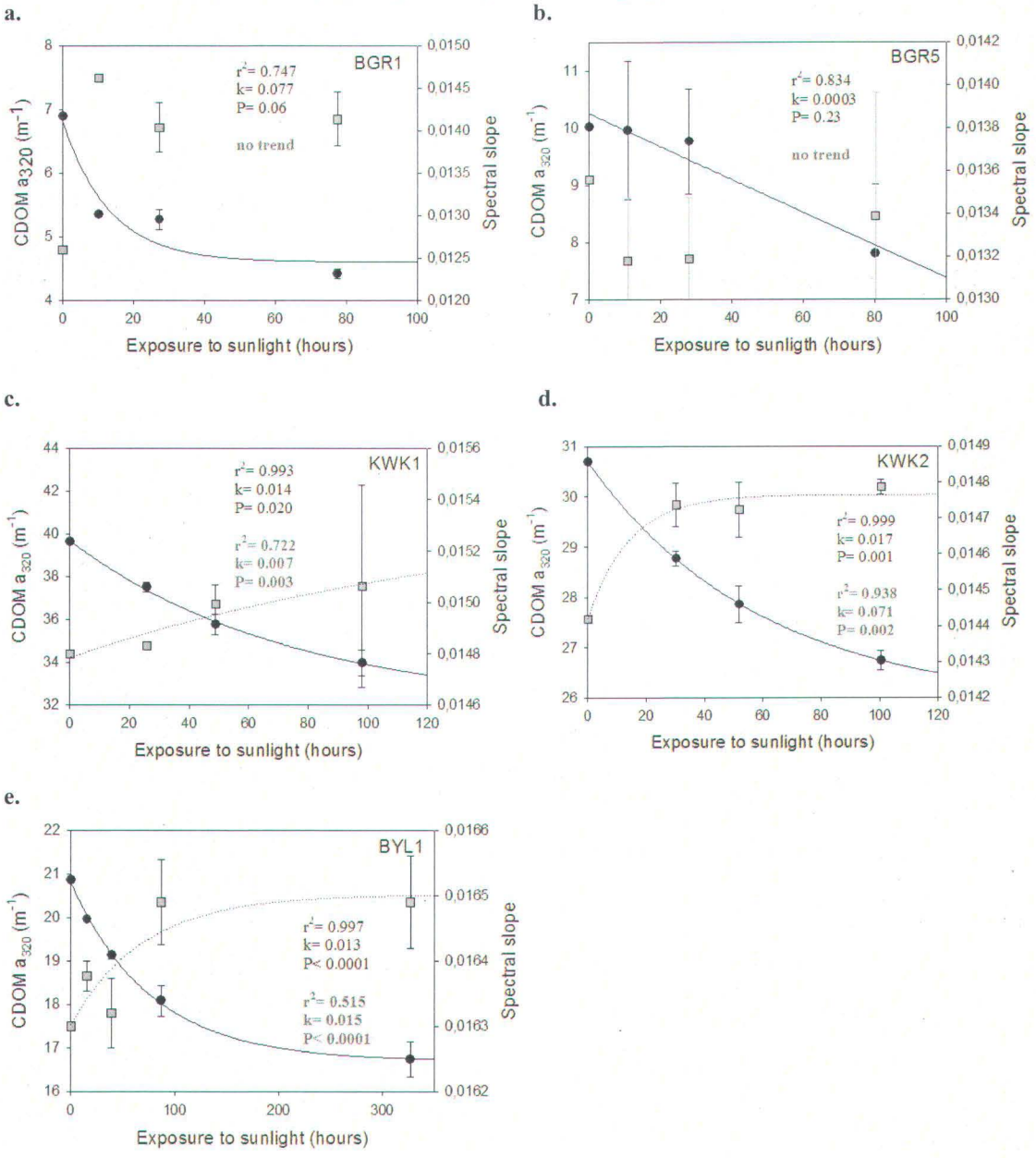


Figure 18: Changes in fluorescence properties of components present in thermokarst ponds and subjected to photochemical degradation, on an absolute scale (solid line) and on a relative basis (dotted line) for the entire experiment:
The lines represesent the difference between mean of triplicates at initial time and mean of triplicates at the end of the experiment.
a.BGR1, b. BGR5, c. KWK1, d. KWK2, e. BYL1. Note that exposure times are not the same in all ponds (refer to Material and Methods).

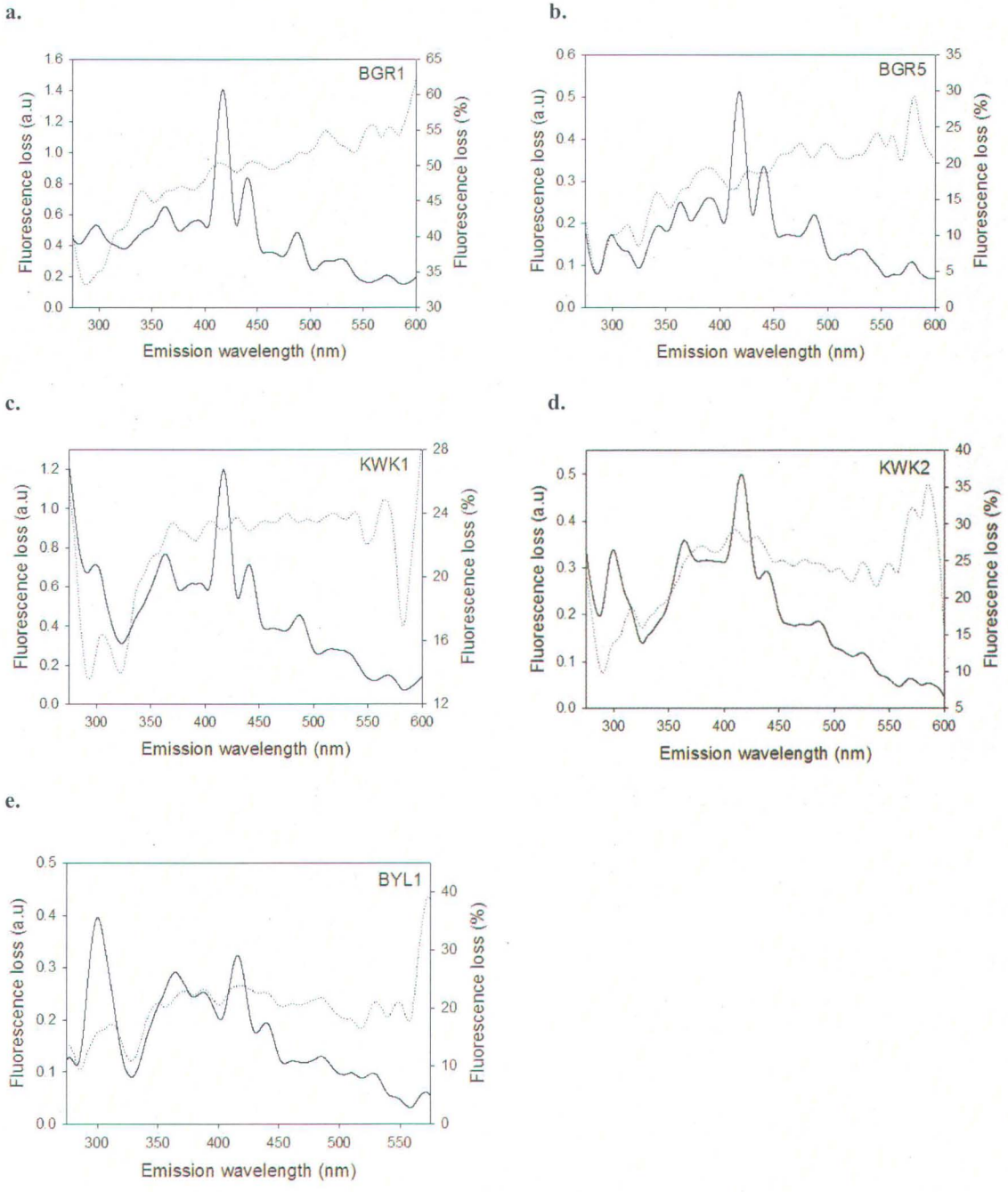


Figure 19: Trends in changes of the humification index HI-1 during 2005 photochemical degradation experiments.

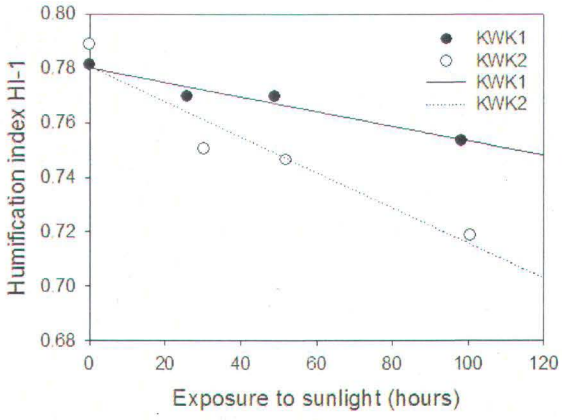


Figure 20: Changes in DOC concentration (black circles, solid line) and specific absorptivity (gray squares, dotted line) during DOM microbial degradation experiments in 2004:
a. KWK3 and **b.** BON4. Mean values of triplicates and r^2, P value and k (slope of curve, exponential or linear, in day^{-1}) of fitted curve (when available) are shown. (DOC regression parameters in black; absorptivity regression parameters in gray).

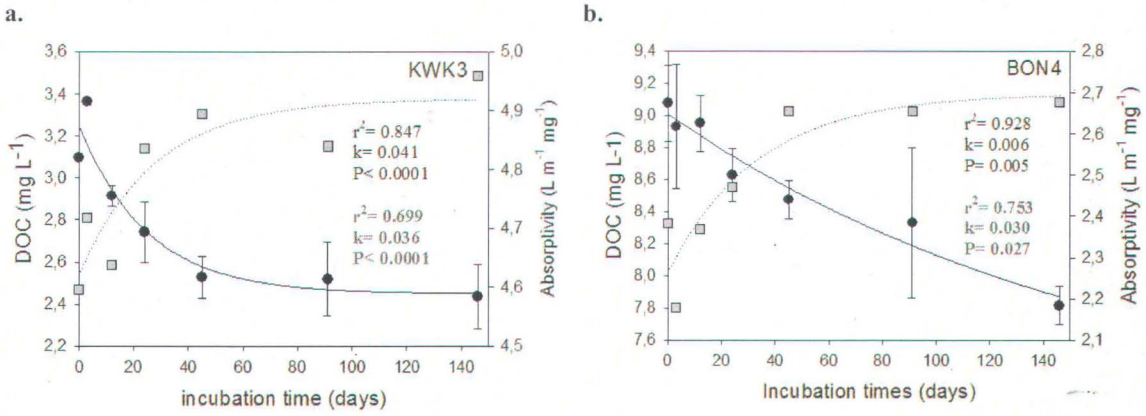


Figure 21: Changes in CDOM a320 (black circles, solid line) and spectral slope (gray squares, dotted line) during DOM microbial degradation experiments in 2004:
a. KWK3 and **b.** BON4. Mean values of triplicates and r^2, P value and k (slope of curve, exponential or linear, in day^{-1}) of fitted curve (when available) are shown. (a_{320} regression parameters in black; spectral slope regression parameters in gray).

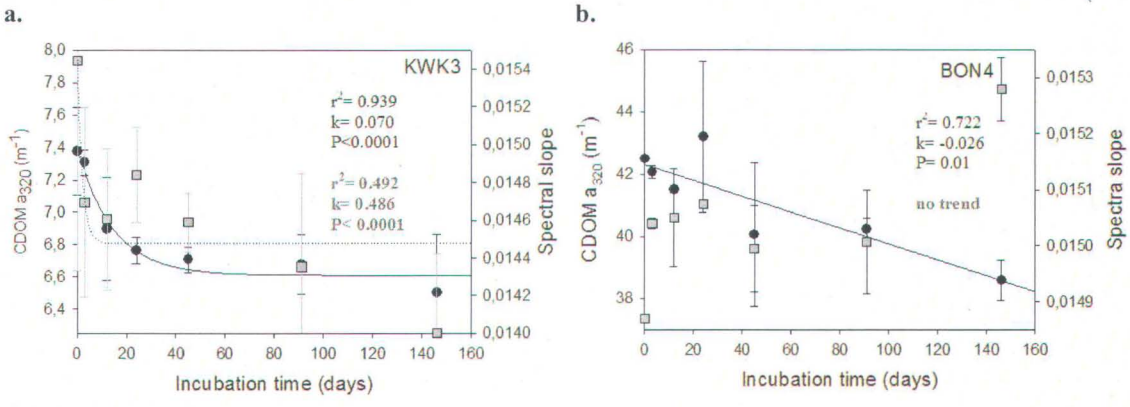


Figure 22: Changes in DOC concentration (black circles, solid line) and absorptivity (gray squares, dotted line) during DOM microbial degradation experiments in 2005:
a. BGR1, **b.** BGR5, **c.** KWK1, **d.** KWK2 and **e.** BYL1. Mean values of triplicates and r^2, P value and k (slope of curve, exponential or linear, in day^{-1}) of fitted curve (when available) are shown. (DOC regression parameters in black; absorptivity regression parameters in gray).

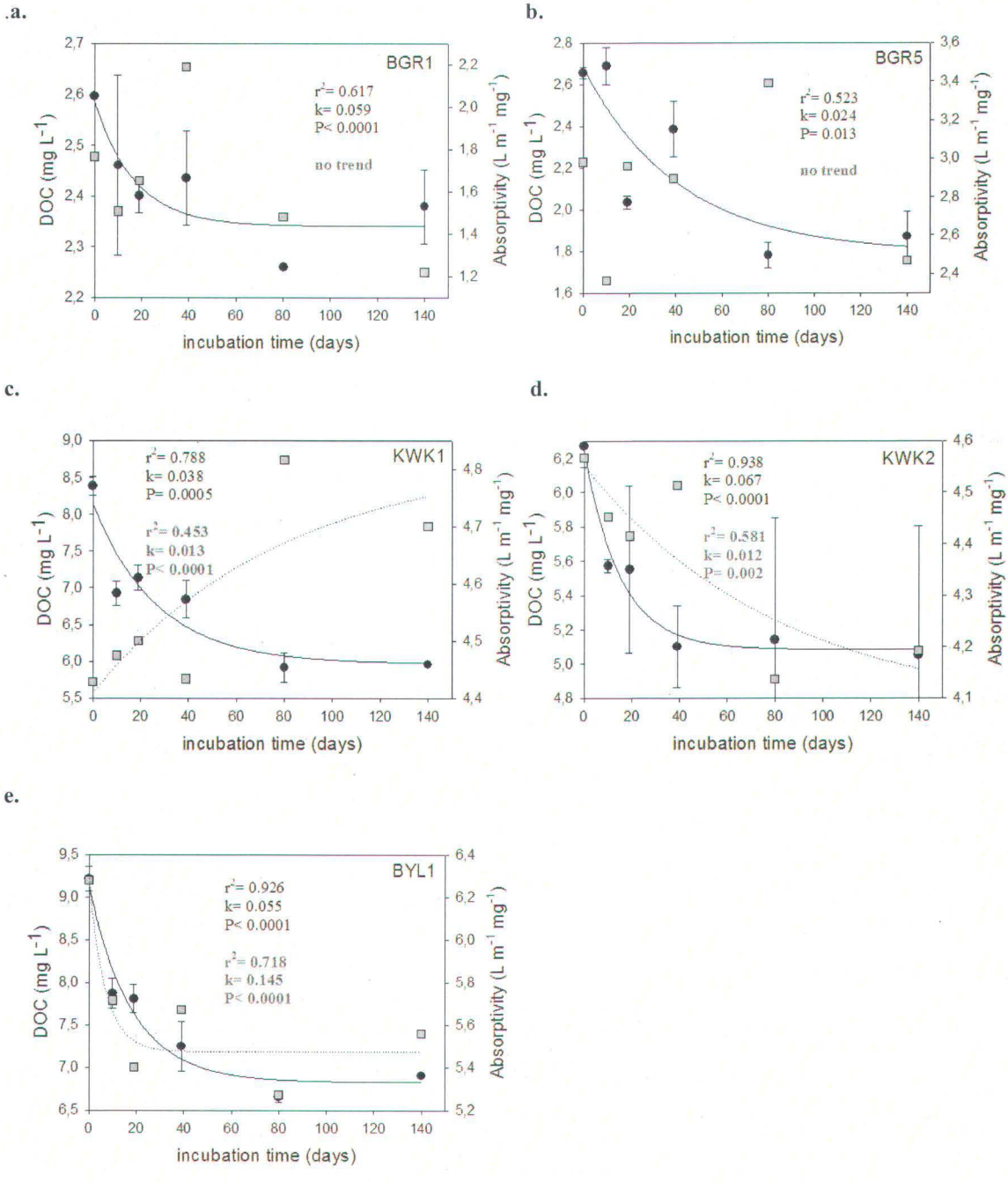


Figure 23: Changes in CDOM a_{320} (black circles, solid line) and spectral slope (gray squares, dotted line) during DOM microbial degradation experiments in 2005:
a. BGR1, **b.** BGR5, **c.** KWK1, **d.** KWK2 and **e.** BYL1. Mean values of triplicates and r^2, P value and k (slope of curve, exponential or linear, in day^{-1}) of fitted curve (when available) are shown. (a_{320} regression parameters in black; spectral slope regression parameters in gray).

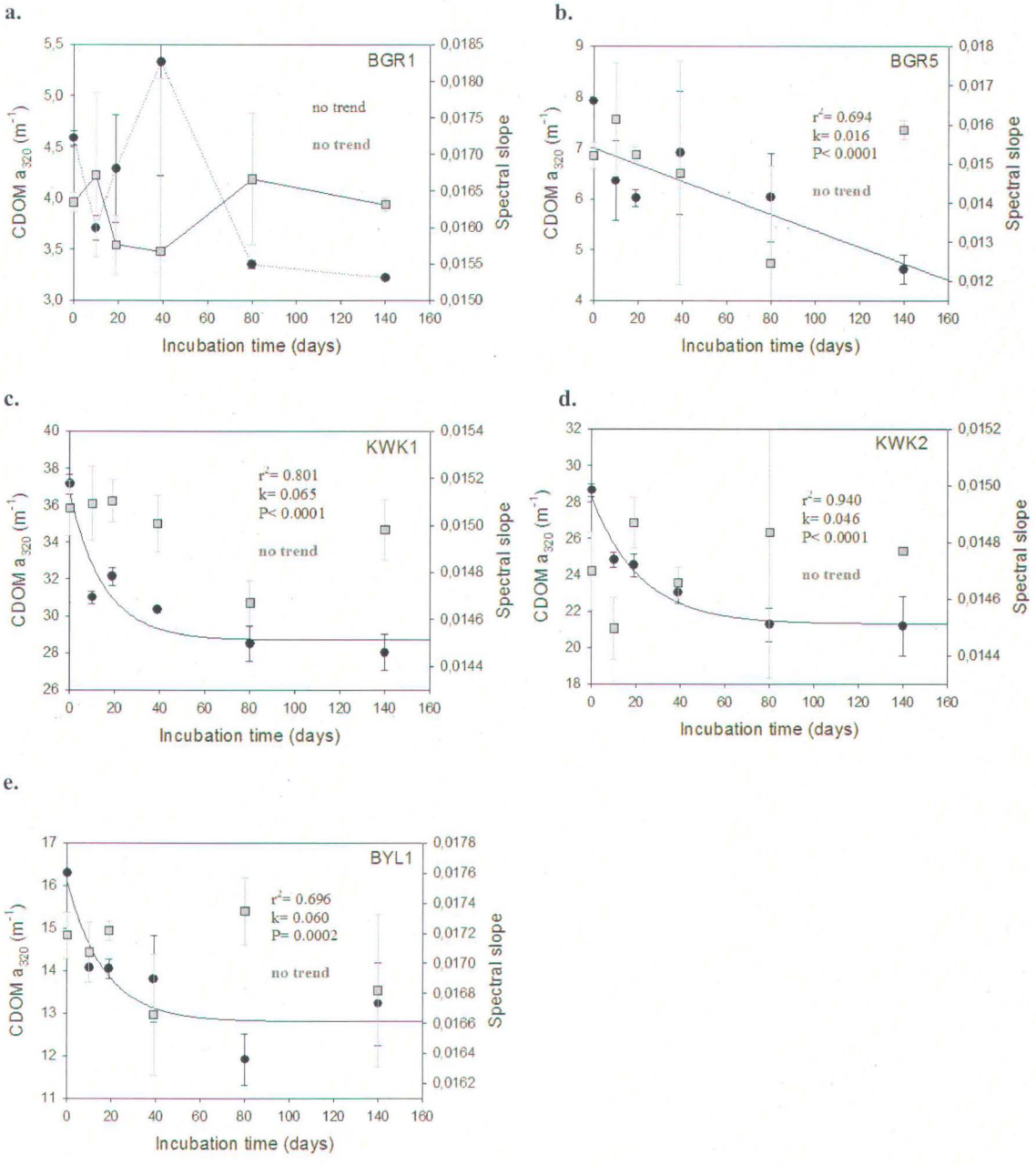


Figure 24: Changes in fluorescence properties of components presented in thermokarst ponds after having been subjected to microbial degradation for 140 days on an absolute scale (solid line) and on a relative basis (dotted line):
The lines represesent the difference between mean of triplicates at the beginning and end of the experiment. a.BGR1, b. BGR5, c. KWK1, d. KWK2, e. BYL1.

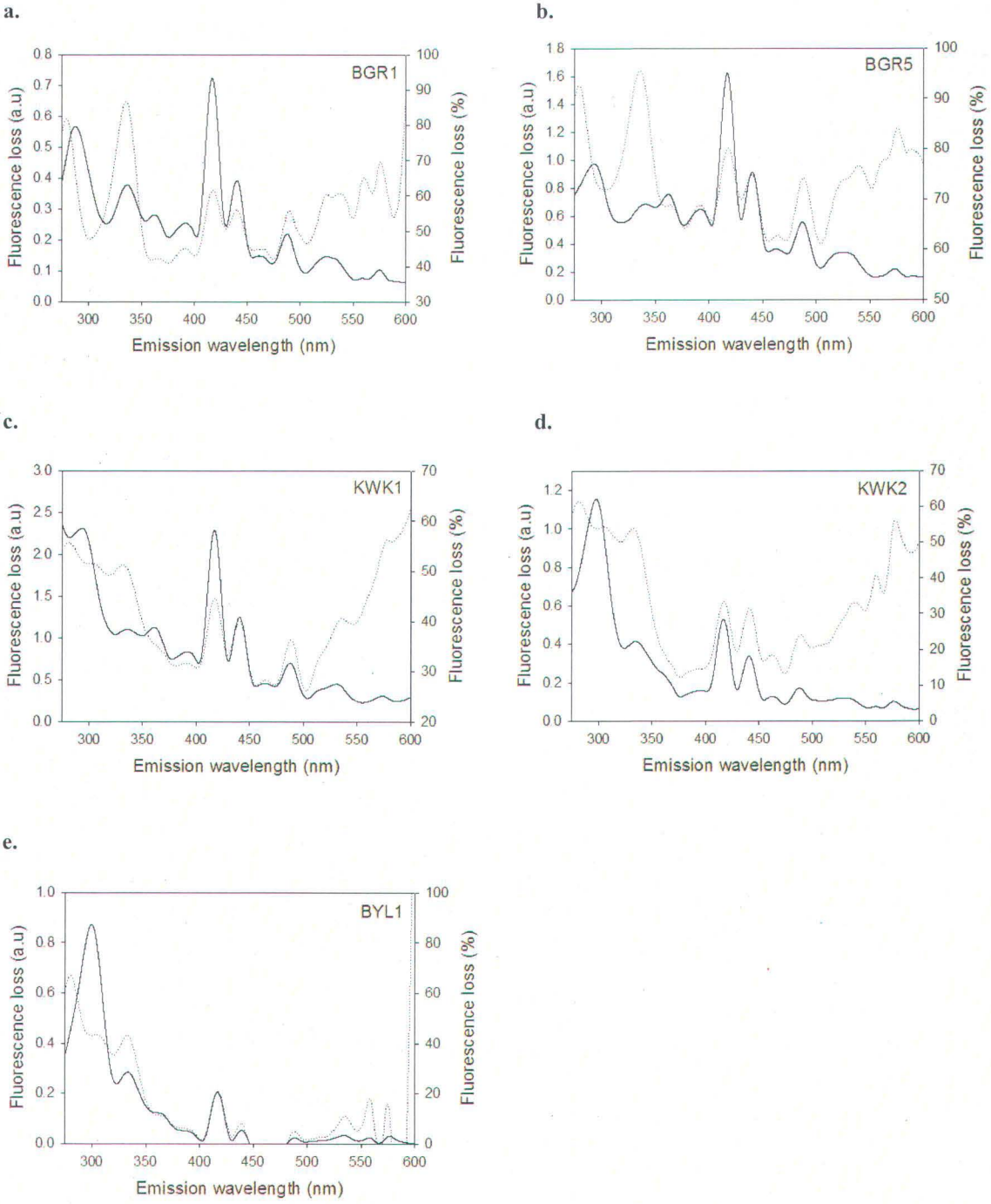


Figure 25: Trends in changes of the humification index HI-1 during the 2005 microbial degradation experiments.

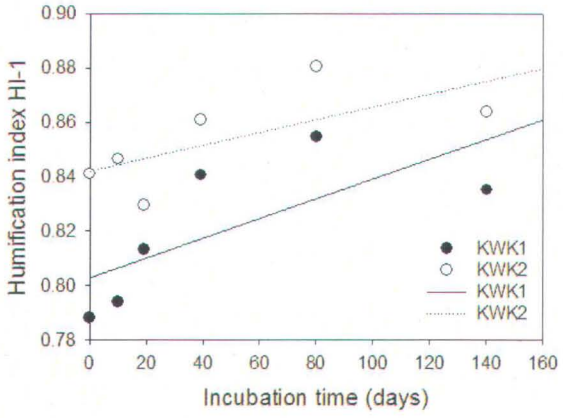


Table 9: Physicochemical and biological data gathered from limnological characterizations of the studied thermokarst ponds

Pond name	Date	Surface water temperature (°C)	Maximum depth (m)	pH*	TSS solids (mg L^{-1})	Conductivity (µS cm^{-1})	Dissolved oxygen (%)	Nutrients				DOC (mg L^{-1})
								NH_4 (µg N L^{-1})	*NO_3*	*TP* (µg P L^{-1})	*PO_4*	
bgr1	11/07/2005	20.9	3.3	7.1	5.3	n.a	106	62.2	21.0	26.7	2.0	2.5
bgr5	11/07/2005	19.9	2.0	6.4	15.5	n.a	97	n.a	n.a	63.4	n.a	4.7
kwk1	19/07/2005	24.2	2.2	6.9	9.4	31	95	53.5	10.8	79.3	2.9	9.0
kwk2	19/07/2005	24.1	3.0	6.4	3.9	30	93	45.3	46.5	49.9	3.0	7.1
kwk3	01/07/2004	18.6	2.8	7.1	7.8	31	n.a	66.0	n.a	37.8	10.0	3.4
bon4	21/07/2004	11.0	< 1	5.1	3.5	14	n.a	46.0	n.a	22.5	1.0	9.3
byl1	29/07/2005	12.6	0.6	9.2	2.0	48	116	67.2	60.6	25.4	<1	9.4
		Temp.	Depth	pH	TSS	Conductivity	DO	NH_4	NO_3	TP	PO_4	DOC
Minimum		11.0	0.6	5.1	2.0	14	93	45.3	10.8	22.5	1.0	2.5
Maximum		24.2	3.3	9.2	15.5	48	116	67.2	60.6	79.3	10.0	9.4
Median		19.9	2.5	6.9	5.3	31	97	57.9	33.7	37.8	2.9	7.1
Mean		18.8	2.3	6.9	6.8	31	101	56.7	34.7	43.6	3.8	6.5
stdev		5.2	1.0	1.2	4.6	12	10	9.8	22.9	21.6	3.6	2.9
N		7	6	7.0	7.0	5	5	6.0	4.0	7.0	5.0	7.0

Pond name	a_{CDOM} 320 nm (m^{-1})	Spectral slope (S)	Absorptivity m^{-1} $(mg\ L^{-1})^{-1}$	FI[1]	Humification index[2] HI-1 *400/360*	HI-2 *470/360*	Bacteria abundance (10^6 cells mL^{-1})	Bacterial production (pmol leu L^{-1} h^{-1})	Chlorophylle *a* ($\mu g\ L^{-1}$)	Dissolved gas CO_2 (ppmv)	CH_4 (ppmv)
bgr1	4.46	0.015	1.79	1.36	0.89	0.50	2.0	529	0.4	364	10.0
bgr5	8.79	0.014	1.87	1.18	0.83	0.51	11.6	1195	0.3	949	19.5
kwk1	38.9	0.015	4.31	1.13	0.89	0.61	2.7	243	3.7	926	18.5
kwk2	30.5	0.014	4.32	1.14	0.88	0.58	1.7	203	1.8	1283	37.1
kwk3	10.5	0.013	3.08	n.a	n.a	n.a	7.0	n.a	2.0	750	4.0
bon4	42.2	0.015	4.52	n.a	n.a	n.a	1.3	n.a	3.7	2442	20.7
byl1	20.9	0.016	2.23	1.20	0.85	0.52	3.0	n.a	1.1	275	10.1
	a_{CDOM}	S	absorptivity	FI	Humification index		BA	BP	Chl *a*	CO_2	CH_4
Minimum	4.5	0.013	1.79	1.13	0.83	0.50	1.3	202	0.3	275	4.0
Maximum	42.2	0.016	4.52	1.36	0.89	0.61	11.6	1195	3.7	2442	37.1
Median	20.9	0.015	3.08	1.18	0.88	0.52	2.7	386	1.8	926	18.5
Mean	22.3	0.015	3.16	1.20	0.87	0.54	4.2	542	1.8	999	17.1
stdev	15.2	0.001	1.22	0.09	0.03	0.05	3.8	459	1.4	726	10.7
N	7	7	7	5	5	5	7	4	7	7	7

n.a = not available

*arbitrary choice of a value among many profiles

[1] MacKnight et al. 2001

[2] Kalbitz et al. 1999

Table 10: Change in DOC and color and estimation of daily mineralization rates during photochemical degradation of dissolved organic matter in the 2005 experiments

Pond name		DOC				Color (a_{320})		
initial DOC	*in situ* exposure	mean	loss mean	mean	daily mineralization*	mean	loss mean	
a_{320}	(h)	(mg C L^{-1})		(%)	(mg C m^{-3} d^{-1})	(m^{-1})	(m^{-1})	(%)
BGR1								
2.93	10.1	2.81	0.12	4		5.4	1.5	22
6.892	27.3	2.60	0.33	11	288	5.3	1.6	24
	77.5	2.58	0.35	12		4.4	2.5	36
BGR5								
3.36	10.8	3.09	0.27	8		10.5	-0.5	-5
10.0	28.0	3.21	0.14	11	120	9.8	0.3	3
	80.2	2.82	0.54	14		7.8	2.2	22
KWK1								
8.63	25.8	8.40	0.23	3		37.5	2.1	5
39.64	48.9	8.05	0.58	7	290	35.8	3.9	10
	98.1	7.98	0.65	8		34.0	5.7	14
KWK2								
7.53	30.3	6.5	1.0	13		28.8	1.9	6
30.7	51.9	6.4	1.2	15	550	27.9	2.8	9
	100	6.4	1.1	14		26.7	4.0	13
BYL1								
9.37	15.4	9.8	-0.4	-4		20.0	0.9	4
20.9	39.2	9.9	-0.5	-5	0	19.1	1.7	8
	86.9	9.2	0.2	2		18.1	2.8	13
	327	8.9	0.4	5		16.7	4.1	20

*estimated from the second sampling with mean loss in absolute value

Table 11: Changes in DOC and color and estimation of the labile reservoir of DOC during microbial degradation experiments in 2004 and 2005

Pond name		DOC					Color (a_{320})		
			loss		DOC_L*			loss	
initial DOC	day	mean	mean	mean			Mean	mean	
Initial a_{320}		(mg C L^{-1})		(%)	(mg C L^{-1})	(%)	(m^{-1})	(m^{-1})	(%)
2004									
BON4	3	8.93	0.15	2	0.23	2	42.1	0.4	1
9.08	12	8.95	0.13	1			41.5	1.0	2
42.5	24	8.63	0.45	5			43.2	-0.7	-2
	45	8.47	0.60	7			40.1	2.4	6
	91	8.33	0.75	8			40.2	2.3	5
	146	7.82	1.26	14			38.6	3.9	9
KWK3	3	3.36	-0.27	-9	0.19	6	7.3	0.1	1
3.10	12	2.91	0.18	6			6.9	0.5	6
7.4	24	2.74	0.35	11			6.8	0.6	8
	45	2.53	0.57	18			6.7	0.7	9
	91	2.52	0.58	19			6.7	0.7	9
	146	2.44	0.66	21			6.5	0.9	12
2005									
BGR1	10	2.46	0.14	5	0.15	6	3.7	0.9	19
2.60	19	2.60	0.00	8			4.3	3.1	67
4.6	39	2.43	0.16	6			5.3	2.0	45
	80	2.26	0.34	13			3.3	4.0	88
	140	2.38	0.22	21			3.2	4.2	91
BGR5	10	2.69	-0.03	-1	0.23	9	6.4	1.6	20
2.66	19	2.03	0.62	23			6.0	1.9	24
7.9	39	2.39	0.27	10			6.9	1.0	13
	80	1.78	0.88	33			6.0	1.9	24
	140	1.87	0.79	30			4.6	3.3	42
KWK1	10	6.93	1.45	17	1.10	13	31.0	6.1	17
8.37	19	7.14	1.24	15			32.1	5.0	13
37.133	39	6.85	1.53	18			30.4	6.8	18
	80	5.93	2.45	29			28.5	8.6	23
	140	5.96	2.41	29			28.0	9.1	25
KWK2	10	5.57	0.70	11	0.73	12	24.8	3.8	13
6.27	19	5.55	0.72	16			24.5	4.1	14
29	39	5.10	1.17	19			23.0	5.6	20
	80	5.14	1.13	24			21.3	7.4	26
	140	5.05	1.22	28			21.2	7.5	26
BYL1	10	7.87	1.35	15	1.15	13	14.1	2.2	14
9.22	19	7.81	1.41	15			14.0	2.3	14
16.3	39	7.25	1.97	21			13.8	2.5	15
	80	6.66	2.56	28			11.9	4.4	27
	140	6.91	2.31	25			13.2	3.1	19

*Results from computation of remaining DOC after 14 days in our models

Table 12: Comparisons between rates of photochemical and microbial degradation in five thermokarst ponds in surface waters

Pond name	Photobleaching DOC decrease rates			Microbial degradation DOC decrease rates
	h^{-1}	d^{-1}		d^{-1}
BGR1	0.0590	1.416	>>	0.0593
BGR5	0.0057 (linear)	0.137	>	0.0241 (exponential)
KWK1	0.0213	0.511	>>	0.0375
KWK2	0.0720	1.728	>>	0.0667
BYL1	0.0210 (linear)	0.504	>	0.0550 (exponential)

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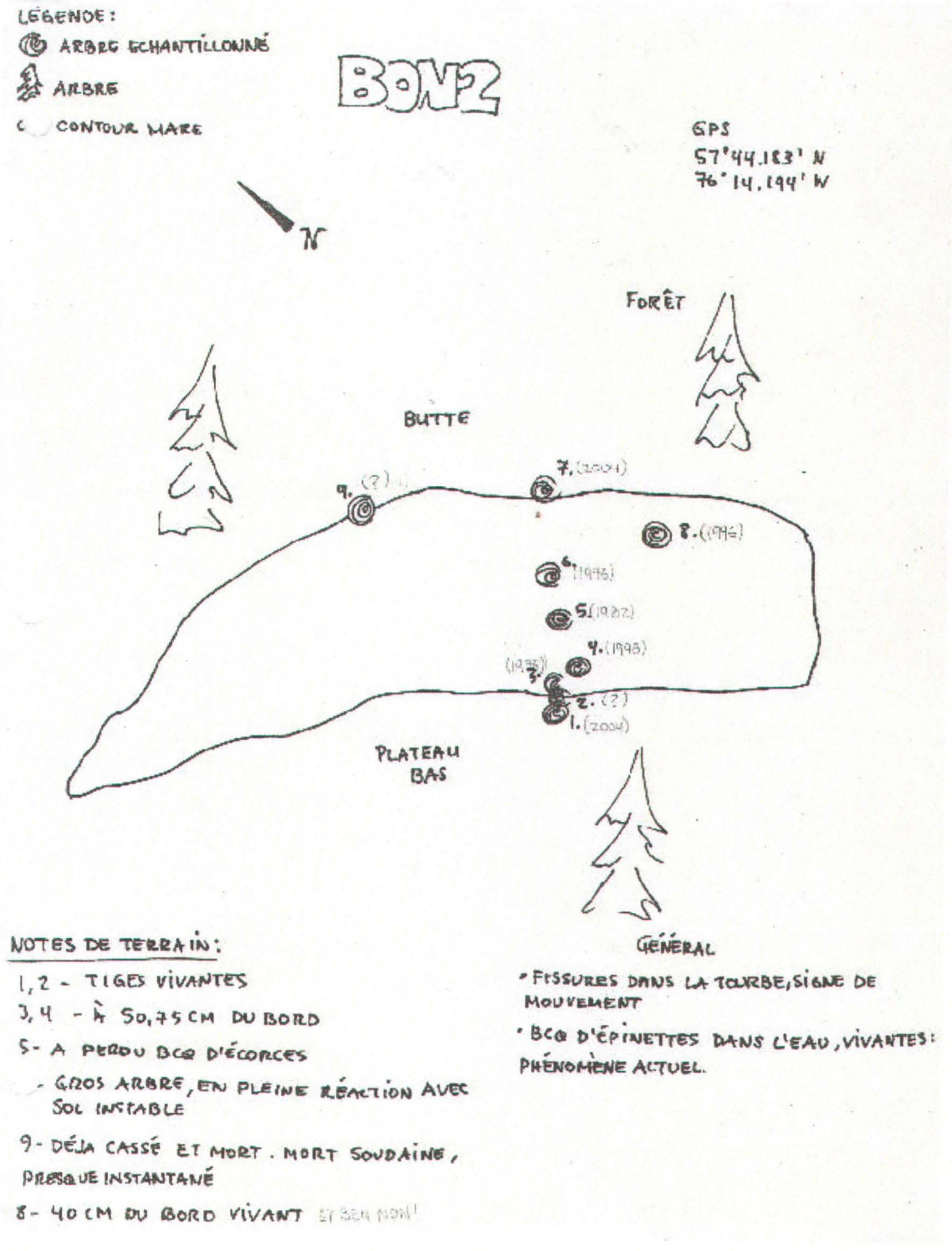
Annexes

Annexe 1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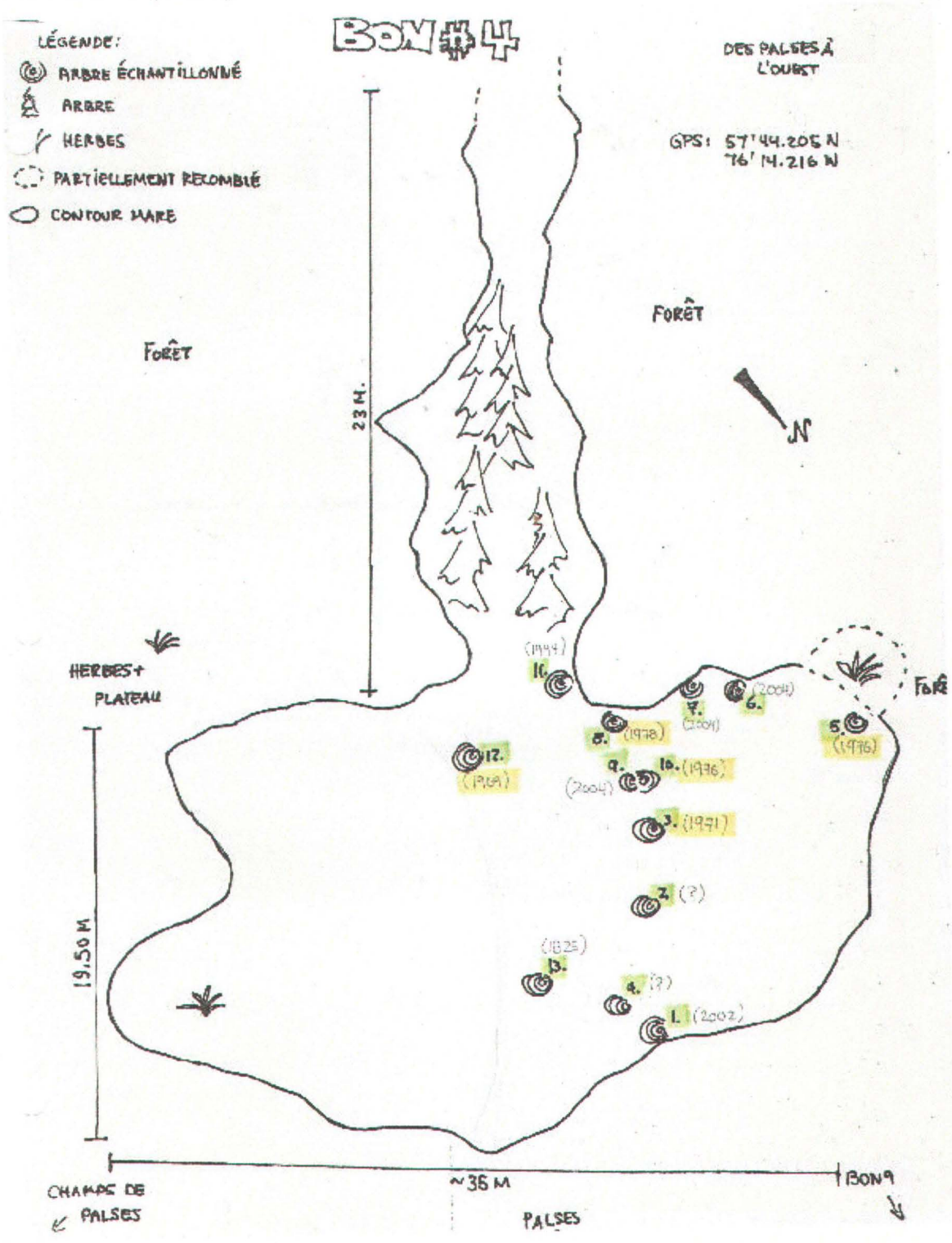
PLATEAU BAS
NOTES DE TERRAIN :
1, 2 - TIGES VIVANTES
3, 4 - À 50,75 CM DU BORD
5 - A PERDU BCQ D'ÉCORCES
- GROS ARBRE, EN PLEINE RÉACTION AVEC SOL INSTABLE
9 - DÉJÀ CASSÉ ET MORT. MORT SOUDAINE, PRESQUE INSTANTANÉ
8 - 40 CM DU BORD VIVANT ET BIEN NON!
GÉNÉRAL
• FISSURES DANS LA TOURBE, SIGNE DE MOUVEMENT
• BCQ D'ÉPINETTES DANS L'EAU, VIVANTES: PHÉNOMÈNE ACTUEL.

Annexe 1 (suite)



Annexe 2

Chercheur : Isabelle Laurion Adresse: 2390, Einstein, C.P. 7500, Québec, G1V 4C7
Institution: INRS-ETE Téléph: 654-2524, 654-2521
requête: 04-05 17-EX-IL-1-O Nombre d'échantillons: 18
compte: 13C55 Soumission: 21-août-2004 Sortie: 2004-07-28

# Delta-Lab	# client	Matrice	d15N	Précision	d13C	Précision	Prix
04-05 17-EX-IL-1-O-S1	BGR1	CO2			-15,7		
04-05 17-EX-IL-1-O-S2	BGR2	CO2			-22,1		
04-05 17-EX-IL-1-O-S3	BGR3	CO2			-15,7		
04-05 17-EX-IL-1-O-S4		C1-C5			nM		
04-05 17-EX-IL-1-O-S5	BGR4	CO2			-12,8		
04-05 17-EX-IL-1-O-S6		C1-C5			nM		
04-05 17-EX-IL-1-O-S7	BGR8	CO2			-9,8	0,1	
04-05 17-EX-IL-1-O-S8	VD-1	CO2			-18,5		
04-05 17-EX-IL-1-O-S9	KUU1	CO2			-12,7		
04-05 17-EX-IL-1-O-S10	KUU3	CO2			-13,2		
04-05 17-EX-IL-1-O-S11	KUU4	CO2			-17,5		
04-05 17-EX-IL-1-O-S12		C1-C5			nM		
04-05 17-EX-IL-1-O-S13	KUU5	CO2			-19,2		
04-05 17-EX-IL-1-O-S14		C1-C5			nM		
04-05 17-EX-IL-1-O-S15	KUU6	CO2			-12,8		
04-05 17-EX-IL-1-O-S16	BCN1	CO2			-16,4	0,2	
04-05 17-EX-IL-1-O-S17	BCN2	CO2			19,23C?	0,04	
04-05 17-EX-IL-1-O-S18	BCN4	CO2			-17,0		
04-05 17-EX-IL-1-O-S19		C1-C5			nM		
04-05 17-EX-IL-1-O-S20	BCN5	CO2			-16,9		
04-05 17-EX-IL-1-O-S21		C1-C5			nM		
04-05 17-EX-IL-1-O-S22	BCN6	CO2			-16,7	0,1	
04-05 17-EX-IL-1-O-S23	BCN7	CO2			-21,2	Lpc	
04-05 17-EX-IL-1-O-S24	BCN8	CO2			-17,1		

	Theoretical	Measured		
CGC-RFF	-43,6	-43,6	± 0,4	(n=7)

* Also, the in-house d13C value for CH4 for this sample

Modalités

1 La CGC-Québec (Delta-Lab) exécute en entier les travaux visés par la proposition avec diligence.

2 La CGC-Québec garde secret et ne divulgue pas aux tiers les renseignements reliés à la demande, et protège ces renseignements à de bonnes pratiques scientifiques et techniques. Toutefois, la CGC-Québec ne prend aucun engagement et ne donne aucune garantie en ce qui concerne les résultats découlant des travaux, explicitement ou implicitement en application de la loi ou autrement, notamment des garanties implicites touchant la qualité marchande ou la convenance à un usage particulier.

3 L'institution détient entière propriété intellectuelle relative aux résultats de la présente demande. Les scientifiques du Delta-Lab s'engagent à ne pas divulguer aux tiers les résultats des travaux d'analyse.

4 Le demandeur exonère et indemnise Ressources naturelles Canada, ses employés et mandataires à l'égard de tout dommage-intérêt, réclamation, demande, perte, coût, y compris les honoraires d'avocats, poursuites ou procédures se rapportant de quelque manière que ce soit à l'utilisation des produits à livrer ou à une perte de ceux-ci. Ressources naturelles Canada se réserve le droit de se défendre contre une telle action ou procédure et de choisir son avocat.

5 Le demandeur s'abstient qu'il ne divulgue ou fourni à la CGC-Québec tout renseignement protégé d'un tiers sans autorisation, échantillon ou document se rapportant aux travaux.

6 L'institution (le demandeur) ne doit pas utiliser le nom de Ressources naturelles Canada ou le nom de l'un des membres de son personnel en ce qui concerne l'interprétation des résultats sans consultation préalable. Lors de publication, l'institution (le demandeur) peut mentionner le nom du Delta-Lab comme laboratoire d'analyse.

7 Pour être valide, toute modification à la présente entente doit être constatée par écrit et signée par les représentants autorisés des parties.

8 Les parties ne sont pas responsables de l'interruption qui survient dans l'exécution des obligations visées par la présente entente en raison de circonstances en dehors de leur contrôle, notamment un cas fortuit, des troubles industriels ou une mesure gouvernementale.

9 La présente entente est régie et interprétée conformément aux lois de la province de Québec et du Canada applicables et elle est traitée comme une demande de travaux.

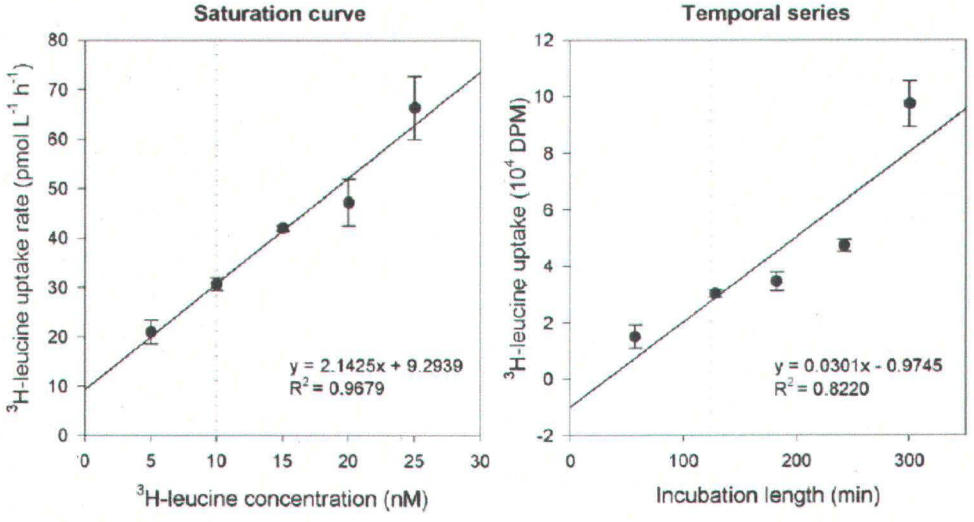
10 L'institution et la CGC-Québec doivent tenter de régler tout différend découlant de la présente entente ou lié à l'application de celle-ci en recourant à la procédure décrite dans les dispositions relatives aux méthodes privilégiées du règlement des différends pour les contrats généraux des ministères de Ressources naturelles Canada afin de réduire, pour les deux parties, les délais et les dépenses liés aux litiges.

11 Pour que l'INRS en soit avisée à la facturation, l'institution (le demandeur) retourne par télécopie la présente page signée en guise d'acceptation des travaux effectués à CGC-Q, M/S Brigitte Lafortune, 418 654 2615 ou par courriel: blafortune@nrcan.gc.ca.

12 Le demandeur doit acquitter tous les coûts approuvés pour les travaux visés par la demande dans les trente (30) jours de la date de la facture. Le paiement se fait par chèque établi à l'ordre du Receveur général du Canada. La commande doit être envoyée à l'adresse suivante: Ressources naturelles Canada, M/S: Lafortune, Bureau 840, 880 Chemin Ste-Foy, C.P. 7500, Québec (Qc), G1V 4C7. La CGC-Québec se réserve le droit de charger, sur les comptes en souffrance, des intérêts de trois (3) pour cent par année en sus du taux préférentiel établi par la Banque du Canada.

Annexe 3

Annex 2.3 Saturation curve and temporal series for the calibration of the ^{3}H-leucine uptake measurements. The measurements were made on water from the Great Whale River sampled on July 19th from the shore upstream of the Cris dock. The error bars represent the analytical standard deviation of the method (n = 3). The dotted lines show the ^{3}H-leucine concentration and the incubation length used during the present study.



Data from Vallières 2007

Annexe 4

nom mare	TOTAL Prelim calcul mg TSS/L	ORG volatiles calcul TSS org (mg/L)	FIXED fixés calcul TSS fixés (mg/L)	RATIO org/total		description
bgr1	23,8	6	15,4	0,3	bgr1	thermok. Pond
bgr1-surface	5,3	0,9	4,4	0,2	bgr1-surface	thermok. Pond
bgr2	271	18,3	253	0,1	bgr2	thermok. Pond
bgr3	14,5	9	5,5	0,6	bgr3	thermok. Pond
bgr4	39,7	15,2	24,6	0,4	bgr4	thermok. Pond
bgr5-surface	15,5	2,6	12,9	0,2	bgr5-surface	thermok. Pond
bon1	11,4	15,1	-3,7	1,3	bon1	thermok. Pond
bon2	1,3	2,2	-0,8	1,6	bon2	thermok. Pond
bon3	3,8	4,8	-0,9	1,3	bon3	thermok. Pond
bon4	3,5	7,3	-3,7	2	bon4	thermok. Pond
bon6	1,3	3,9	-2,6	3	bon6	thermok. Pond
bon8	0,7	1,7	-1,0	2,5	bon8	thermok. Pond
bon9	7,3	8,8	-1,4	1,2	bon9	thermok. Pond
byl1	2	2,2	-0,2	1	byl1	thermok. Pond
byl11-surface	7	3,1	3,9	0,4	byl11-surface	thermok. craque
byl12	2,3	1,5	0,8	0,7	byl12	thermok. craque
byl13	3,4	1,8	1,5	0,5	byl13	thermok. craque
byl14	0,4	1,2	-0,8	3,3	byl14	thermok. craque
byl15	1,7	1,4	0,2	0,9	byl15	thermok. Pond
byl16	1	1,8	-0,8	1,9	byl16	thermok. Pond
byl17	5	20,2	-15,2	4	byl17	thermok. Pond
byl18	5,4	10,9	-5,5	2	byl18	thermok. craque

byl2	2,8	2,2	0,6	0,8	byl2	thermok. craque
byl3	10,4	12	-1,7	1,2	byl3	thermok. Pond
byl4	4,9	5	-0,1	1	byl4	thermok. Pond
byl7	24	5,2	18,8	0,2	byl7	thermok. Pond
byl8	11,6	5,9	5,7	0,5	byl8	thermok. Pond
kuj1	5,4	6,1	-0,7	1,1	kuj1	thermok. Pond
kuj3	7,8	6,3	1,4	0,8	kuj3	thermok. Pond
kuj4	158	16,1	142	0,1	kuj4	thermok. Pond
kuj5	2,8	5,4	-2,6	2	kuj5	thermok. Pond
kuj6	11,4	13,2	-1,8	1,2	kuj6	thermok. Pond
kuj7	12,4	5,1	7,3	0,4	kuj7	thermok. Pond
kwk1-surface	9,4	4,1	5,4	0,4	kwk1-surface	thermok. Pond
kwk2-b	64,6	57,3	7,3	0,9	kwk2-b	thermok. Pond en recomblement
kwk2-surface	3,9	3,4	0,5	0,9	kwk2-surface	thermok. Pond
vdt1	2	2,8	-0,8	1,4	vdt1	thermok. Pond