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EFFECTS OF HYDROLOGICAL CONNECTIVITY ON THE ECOLOGY OF ARCTIC LAKES

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DEDICATION

A mis padres
To my parents
A mes parents

FOREWORD

This thesis covers the results of my doctoral research under the supervision of Milla Rautio and Michael Power, prepared under the frame of the doctoral program in biology. This doctoral thesis is presented in three chapters in the form of scientific articles, a general introductory chapter, and final concluding remarks. The first opening chapter is a contextualization of the current knowledge in specific aspects of Arctic limnology addressed in this doctoral research. The three following chapters that are the core of the thesis are written as scientific articles, two of which are published in scientific journals, and the third one is in preparation to be submitted for publication. The first chapter, describing the trophic state of the studied lakes, was published in 2021 in the journal *Arctic Science* as part of a Virtual Special Issue entitled: *Terrestrial Geosystems, Ecosystems, and Human Systems in the Fast-Changing Arctic*, in collaboration with Connie Lovejoy. The second chapter, focusing on the effect of hydrological connectivity on lake metabolism, was prepared in collaboration with Matthew J. Bogard and the support of Guillaume Grosbois, Joseph M. Culp and Vilmantas Prėskienis. It was published in the journal *Global Change Biology* in 2024 and the limnological and metabolic data associated with this publication was also published in 2024 in *Nordicana D*. The third chapter analyzes the carbon transfer at the base of the food web along a depth gradient and is being prepared in collaboration with Conne Lovejoy and Joseph M. Culp. The final chapter summarizes the work of all the thesis in the form of concluding remarks and discusses the contributions of this doctoral work. I have participated as the lead in the conceptualization, sampling, methodology and formal analysis of all the samples used for this project as well as lead author in each of the manuscripts with the support and supervision of professors Milla Rautio and Michael Power. The articles included in this thesis and further details are listed below:

Chapter 1. Trophic state
Title: Evidence of eutrophication in Arctic lakes
Authors: Paola Ayala-Borda, Connie Lovejoy, Michael Power and Milla Rautio
Published on May 13th, 2021, in *Arctic Science* as part of the Virtual Special Issue entitled: *Terrestrial Geosystems, Ecosystems, and Human Systems in the Fast-Changing Arctic*

Chapter 2. Lake metabolism

Title: Dominance of net autotrophy in arid landscape low relief polar lakes, Nunavut, Canada

Authors: Paola Ayala-Borda, Matthew J. Bogard, Guillaume Grosbois, Vilmantas Prėskienis, Joseph M. Culp, Michael Power, Milla Rautio

Accepted for publication on January 17th, 2024, in *Global Change Biology*

Chapter 3. Carbon transfer

Title: Insights into the Influence of Lake Depth and Phytoplankton Composition for Polyunsaturated Fatty Acids in zooplankton of Arctic lakes

Authors: Paola Ayala-Borda, Connie Lovejoy, Joseph M. Culp, Michael Power and Milla Rautio

In preparation

During my doctoral journey I also contributed to the following scientific article:

Title: Sentinel responses of Arctic freshwater systems to climate: linkages, evidence, and a roadmap for future research

Authors: Jasmine E. Saros, Christopher D. Arp, Frédéric Bouchard, Jérôme Comte, Raoul-Marie Couture, Joshua F. Dean, Melissa Lafrenière, Sally MacIntyre, Suzanne McGowan, Milla Rautio, Clay Prater, Suzanne E. Tank, Michelle Walvoord, Kimberly P. Wickland, Dermot Antoniades, Paola Ayala-Borda, Joao Canario, Travis W. Drake, Diogo Folhas, Václava Hazuková, Henriikka Kivilä, Yohanna Klanten, Scott Lamoureux, Isabelle Laurion, Rachel M. Pilla, Jorien E. Vonk, Scott Zolkos, and Warwick F. Vincent.

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Parts of the results of this thesis were also presented as posters or oral presentations in different national and international conferences and are listed below:

Ayala-Borda, P., Lovejoy, C., Power, M. and Rautio. M. *What do zooplankton eat in Arctic lakes?* Poster. ArcticNet Annual Scientific Meeting (ASM2022). Dec 4-8, 2022.

Ayala-Borda, P., Bogard, M. J., Power, M. and Rautio. M. *Net autotrophy dominates in shallow lakes of the Canadian Arctic*. Oral presentation. 36th Congress of the Society of International Limnology (SIL). Aug 7-10, 2022.

Ayala-Borda, P., Bogard, M. J., Power, M. and Rautio. M. *Internal nutrient cycling promotes net autotrophy in small and shallow lakes of the Canadian Arctic.* Annual Symposium of the Interuniversity Research Group in Limnology (GRIL). Mar 14-16, 2022.

Ayala-Borda, P., Bogard, M. J., Power, M. and Rautio. M. *Arctic lakes as potential CO2 sinks on Victoria Island, Nunavut.* Oral presentation. Annual Symposium of the Center for Northern Studies (CEN). Feb 17-18, 2022.

Ayala-Borda, P., Lovejoy, C., Power, M. and Rautio. *Eutrophication in an Arctic lake without direct human influence: case of lake ERA5 in Cambridge Bay, Nunavut*. Oral presentation. Arctic Change 2020. Dec 7-10, 2020.

Ayala-Borda, P., Lovejoy, C., Power, M. and Rautio. *Première preuve d'un lac arctique eutrophe.* Poster. Annual Symposium of the Interuniversity Research Group in Limnology (GRIL). Mar 12-14, 2020.

Ayala-Borda, P., Lovejoy, C., Power, M. and Rautio. *Première preuve d'un lac arctique eutrophe.* Poster. Annual Symposium of the Center for Northern Studies (CEN). Feb 13-14, 2020.

Ayala-Borda, P., Grosbois, G., Lovejoy, C., Culp, J. M., Power, M. and Rautio. *Limnology of the Greiner Lake watershed lakes and ponds, Cambridge Bay – Nunavut.* Poster. Annual Symposium of the Center for Northern Studies (CEN). Feb 6-8, 2019.

Ayala-Borda, P., Grosbois, G., Lovejoy, C., Culp, J. M., Power, M. and Rautio. *Phytoplankton of the Greiner Lake watershed lakes and ponds, Cambridge Bay - Nunavut.* Poster. Annual Symposium of the Interuniversity Research Group in Limnology (GRIL). Mar 15-16, 2019.

Ayala-Borda, P., Grosbois, G., Lovejoy, C., Culp, J. M., Power, M. and Rautio. *Limnology of the Greiner Lake watershed lakes and ponds, Cambridge Bay – Nunavut.* Poster. ArcticNet Annual Scientific Meeting (ASM2018). Dec 10-14, 2018.

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ABBREVIATIONS

$[^{14}C]$-HCO_3	^{14}C labelled bicarbonate
$[^{3}H]$-leucine	Tritium labelled leucine
°C	Degree celsius
μg	Microgram
μL	Microliter
μS	Microsiemens
a_{320}	Absorption coefficient at 320 nm
a_{440}	Absorption coefficient at 440 nm
acc w_i	Cumulative Akaike weight
AF_{atm}	Atomic fractions for atmosphere
AF_{DO}	Atomic fractions for dissolved oxygen
AF_{H2O}	Atomic fractions for water
AICc	Aikaike information criterion
ANOVA	Analysis of variance
ASV	Amplicon sequencing variant
ATV	All-terrain vehicle
BP	Bacterial production
C	Carbon
C1	Percentage of component1 from PARAFAC
C2	Percentage of component2 from PARAFAC
C3	Percentage of component3 from PARAFAC
C4	Percentage of component4 from PARAFAC
CDOM	Chromophoric dissolved organic matter
CHARS	Canadian high arctic research station
Chl *a*	Chlorophyll *a*
Cm	Centimeter
CO_2	Carbon dioxide
d	Day
d-excess	Deuterium excess
DHA	Docosahexaenoic acid
DIC	Dissolved inorganic carbon
DO	Dissolved oxygen concentration
DOC	Dissolved organic carbon
DOM	Dissolved organic matter
DO_{sat}	Dissolved oxygen saturation
DW	Dry weigh
eDNA	Environmental DNA

EEMs	Excitation-emission matrices
EPA	Eicosapentaenoic acid
ER	Respiration per volume of water
FDOM	Fluorescent dissolved organic matter
GHG	Greenhouse gas
GMWL	Global meteoric water line
GPP	Gross primary production per volume of water
GPP:ER	Gross primary production to ecosystem respiration ratio
h	Hour
ha	Hectare
HCl	Hydrochloric acid
HSD	Honestly significant difference
k_{600}	Gas transfer velocity derived from wind speed
Kd	Light attenuation coefficient
kg	Kilogram
km^2	Square kilometers
k_{O_2}	Temperature specific gas exchange coefficient
L	Liter
LA	Lake area
LEL	Local evaporation line
LMWL	Local meteoric water line
m	Meter
mL	Milliliter
MLR	Multiple linear regressions
mm^3	Cubic millimeter
N	Normal
NEP	Net ecosystem production
nM	Nanomolar
NMDS	Non-metric multidimensional scaling
P	Phosphorus
PAR	Photosynthetic active radiation
PARAFAC	Parallel factor analysis
PCA	Principal component analysis
PERMANOVA	Permutational multivariate analysis of variance
P_{max}	Maximum primary production
PUFA	Polyunsaturated fatty acid
R_x	Ratio of heavy to light isotopes in the sample (x)
S_{289}	Spectral slope for 279-299 nm
Sc	Temperature-specific Schmidt number
$SUVA_{254}$	Specific ultraviolet absorbance at 254 nm

TCA	Trichloroacetic acid
TDP	Total dissolved phosphorus
T-MOSAiC	Terrestrial Multidisciplinary distributed Observatories for the Study of Arctic Connections
TN	Total nitrogen
TN:TP	Molar TN:TP ratio
TP	Total phosphorus
TSI	Trophic state index
U_{10}	Wind speed at 10 m
VPDB	Vienna pee dee belemnite
VSMOW	Vienna standard mean ocean water
w_i	Akaike weights
y	Year
z	Mean depth
Z_{mix}	Lake mixing depth, in this study equal to mean depth
α_g	Fractionation factor associated with gas exchange at the air-water interface
α_p	Fractionation factor associated with photosynthetic dissolved oxygen production from water
α_s	Fractionation factor associated with gas solubility effects
$\delta^{13}C$	Delta carbon 13
$\delta^{15}N$	Delta nitrogen 15
$\delta^{18}O\text{-}H_2O$	Delta oxygen 18 from water
$\delta^{18}O\text{-}O_2$	Delta oxygen 18 from dissolved oxygen
$\delta^{2}H\text{-}H_2O$	Delta deuterium from water
Σw_i	Variable importance cumulative weights

RÉSUMÉ

Le changement climatique affecte les écosystèmes du monde entier, mais l'amplification arctique fait de l'Arctique l'un des environnements qui évoluent le plus rapidement et donc l'un des plus vulnérables. Les changements qui se produisent dans l'Arctique ont un impact non seulement sur la flore, la faune et les communautés humaines locales, mais ils devraient également avoir un effet de rétroaction à l'échelle mondiale à long terme. Il est essentiel de comprendre les processus qui régissent les changements observés dans l'Arctique et les points critiques du changement pour déterminer les stratégies d'adaptation au fur et à mesure que le changement climatique progresse. Les lacs arctiques, en tant qu'éléments intégrateurs du paysage, nous permettent de déterminer les changements qui se produisent dans le paysage environnant. Par conséquent, l'étude des lacs arctiques en combinaison avec leurs bassins versants peut contribuer à la détection précoce des changements régionaux. Les indicateurs des changements dans les lacs arctiques sont les communautés planctoniques qui, par leur composition spécifique et leurs voies métaboliques de traitement du carbone, sont les premières à réagir aux altérations de l'environnement. Cependant, les informations disponibles sur les écosystèmes d'eau douce de l'Arctique et leur fonctionnement sont limitées, et l'on en sait encore moins sur l'effet de la connectivité hydrologique le long du bassin versant. Dans ce travail de doctorat, 35 lacs du bassin versant du lac Greiner, au Nunavut, ont été étudiés pour déterminer leur état trophique et métabolique, ainsi que les mécanismes de transfert du carbone à la base du réseau trophique, en tenant compte de l'influence de la connectivité hydrologique dans le bassin versant.

La dispersion des lacs, leur position dans le bassin versant (c'est-à-dire en amont, au milieu ou en aval), ainsi que la diversité de leurs tailles et de leurs profondeurs (c'est-à-dire profondeur <1, 1-

10 ou >10 m) constituaient un échantillon représentatif de l'ensemble du bassin versant. Les résultats de cette étude ont révélé que la taille, la profondeur et la position des lacs le long du réseau de connectivité hydrologique, associées aux caractéristiques plates et pauvres en matières organiques du paysage, à l'absence de dégradation du pergélisol et aux taux d'évaporation élevés dans cette région, étaient des facteurs déterminants pour les processus biologiques dans les lacs. L'état trophique des lacs était principalement oligotrophe ou ultraoligotrophe, à l'exception d'un lac eutrophe, ERA5, avec plus de 40 % de cyanobactéries dans le biovolume phytoplanctonique. Un état trophique plus élevé a été constaté dans les lacs déconnectés peu profonds représentant des sites d'eaux d'amont par rapport à des lacs plus grands et connectés sur le plan hydrologique. Le métabolisme des lacs était principalement autotrophe net pour les lacs d'amont et à l'équilibre métabolique dans les lacs plus grands situés en amont et en aval. L'état métabolique positif était associé au recyclage interne des nutriments, notamment du phosphore, de la matière organique autochtone et à une forte pénétration de la lumière. En outre, le zooplancton de tous les lacs dépendait fortement des sources planctoniques (et non des sources benthiques et terrestres) le long du gradient de profondeur-connectivité, mais avec une meilleure qualité d'acides gras disponibles dans les lacs plus profonds (c.-à-d. > 1 m). Les lacs profonds abritaient une plus grande proportion de picoplancton mixotrophe et hétérotrophe, améliorant probablement les ressources en carbone pour le zooplancton.

Les résultats de cette étude soulignent la vulnérabilité des lacs d'amont peu profonds face au réchauffement et à l'augmentation des taux d'évaporation qui en résulte dans cet environnement. Étant donné que les lacs autotrophes peu profonds constituent la principale composante du bassin versant, la perte de ces sites de production nette de matière organique pourrait influencer le bilan carbone local. En outre, le comportement des réseaux alimentaires dans les lacs peu profonds donne

un exemple de ce qui pourrait arriver aux lacs d'une profondeur de 1 à 10 m, ce qui pourrait modifier l'état trophique des lacs et augmenter la teneur en cyanobactéries pauvres en acides gras essentiels, avec des effets en cascade sur le reste du réseau alimentaire. Enfin, cette étude souligne l'importance d'étudier les lacs à l'échelle d'un bassin versant, suggérant de futures études pour envisager l'interaction des lacs avec le paysage, en particulier dans l'Arctique qui est en évolution rapide.

Mots clés : Lacs arctiques, connectivité hydrologique, bassin versant, état trophique, métabolisme lacustre, transfert de carbone, réseau trophique.

ABSTRACT

Climate change is affecting ecosystems worldwide, but Arctic amplification makes the Arctic one of the fastest changing environments and is thus one of the most vulnerable. Changes occurring in the Arctic impact not only local flora, fauna, and human communities, but are also expected to have a feedback effect on a global scale in the long term. Understanding the processes governing the observed shifts in the Arctic and hotspots of change is crucial for determining adaptation strategies as climate change progresses. Arctic lakes as integrators of the landscape allow us to determine changes taking place in the surrounding landscape. Therefore, studying Arctic lakes in combination with their watersheds can help in the early detection of regional shifts. Indicators of changes in Arctic lakes are the planktonic communities, which, through their specific composition and metabolic pathways processing carbon exhibit the first response to alterations in the environment. However, limited information about Arctic freshwater ecosystems and their functioning is available, with even less known about the effect of hydrological connectivity along the watershed. In this doctoral work, 35 lakes in the Greiner Lake watershed, Nunavut, were studied to determine their trophic and metabolic states, as well as the mechanisms of carbon transfer at the base of the food web, considering the influence of hydrological connectivity in the watershed. The dispersion of the lakes, their position in the watershed (i.e., headwater, midstream or downstream), and their diverse sizes and depths (i.e., depth <1, 1-10 or >10 m) were a representative sample of the total watershed. Results from this study revealed that the size, depth, and position of lakes along the hydrological connectivity network, coupled with the flat and organic-poor characteristic of the landscape, the absence of permafrost degradation and the high evaporation rates in this region were important determinants for the biological processes in the lakes. The trophic state of the lakes was mostly oligotrophic or ultraoligotrophic, except for one eutrophic lake ERA5 with more than 40% of cyanobacteria in the phytoplankton biovolume. A higher trophic state was found in shallow disconnected lakes representing headwater sites compared to larger, hydrologically connected lakes. The lake metabolism was mostly net autotrophic for headwater lakes and at metabolic equilibrium in larger midstream and downstream lakes. The positive metabolic state was associated with the internal recycling of nutrients, notably phosphorus, autochthonous organic matter, and high light penetration. Additionally, zooplankton in all lakes heavily relied on planktonic sources (as opposed to benthic and terrestrial sources) along the depth-connectivity gradient, but with higher quality of fatty acids available in deeper lakes (i.e., > 1 m). Deep lakes harbored a larger proportion of mixotrophic and heterotrophic picoplankton, likely upgrading carbon resources for zooplankton.

The findings in this study emphasize the vulnerability of shallow headwater lakes to increasing warming conditions and resulting increasing evaporation rates in this environment. Given that shallow autotrophic lakes are the major component of the watershed, the loss of these sites of net organic matter production could influence the local carbon budget. Also, the behavior of food webs in shallow lakes provides an example of what could happen to lakes in the 1-10 m depth category, potentially changing the trophic state of lakes and increasing the content of cyanobacteria poor in essential fatty acids with cascading effects for the rest of the food web. Finally, this study underscores the importance of studying lakes at a watershed scale, suggesting future studies to contemplate the interaction of lakes with the landscape, especially in the rapidly-changing Arctic.

Keywords: Arctic lakes, hydrological connectivity, watershed, trophic state, lake metabolism, carbon transfer, food web.

INTRODUCTION

0.1 Statement of the problem

The Arctic is one of the most ecologically sensitive regions of the world facing the current unprecedented global warming scenario (Seddon et al., 2016).The rate at which the Arctic is warming is much higher compared to other latitudes, also known as polar amplification (Pithan & Mauritsen, 2014; Stuecker et al., 2018), and it has shown to be between two and seven times faster in different regions of the Arctic (Rantanen et al., 2022). Polar amplification increases the vulnerability of the Arctic that becomes less and less resilient to extreme events (Overland, 2020). As the Arctic keeps warming, winters become shorter and precipitation regimes are altered and thus, snow-pack, ice cover, and permafrost phenology are affected (Hansen et al., 2014). Longer warmer periods promote higher terrestrial primary productivity, adding to the terrestrial vegetation biomass and changing the composition of the landscape, process known as Arctic greening (Berner et al., 2020). However, in certain regions of the Arctic, thawing permafrost is changing the landscape through soil mobilization (Vonk et al., 2015). Thawing permafrost, especially the one lying on ice-rich and organic-rich soils, can provoke soils to collapse, transporting thawed material into the waterbodies (Bröder et al., 2021). Thawing permafrost can also affect hydrological connectivity, as new waterbodies and watercourses are generated, while others can be completely drained (e.g., Andresen & Lougheed, 2015; Kokelj et al., 2021). In a contrasting scenario, other regions of the Arctic characterized by low precipitation rates and organic-poor soils, lakes are less exposed to permafrost thaw, but more exposed to evaporation, concentration of solutes in the water and surface loss (Lewis et al., 2015; Smith et al., 2005). The warming experienced in the Arctic also has consequences on a larger ecological scale, as greening and browning promote the mobilization of carbon in the ecosystem, altering the local carbon budgets (Mcguire et al., 2009; McGuire et al., 2006). Increased degradation rates of organic matter linked to greenhouse gas emissions may ultimately affect the global carbon cycle (Mcguire et al., 2010).

Freshwater ecosystems interconnect the whole landscape through streams. Rivers spread across the watershed, in the end, gathering information of the state of the ecosystem in downstream lakes (Alexander et al., 2018). The state of the landscape is transferred to the state of the lake and can be evidenced in the physical, chemical, and biological composition of collected and transformed materials in the water and the sediments (Vincent, 2018). The deep connection between the terrestrial and aquatic components of the landscape, thus, allow to detect ecosystem changes in freshwater ecosystems faster than what may be evidenced by studying the landscape alone (Vincent et al., 2009). Numerous studies indicate the responses of Arctic lakes to climate warming and changes in the landscape evidenced in the ice and thermal regimes (e.g., Begin et al., 2020), organic and inorganic components (e.g., Frey & Smith, 2005; Tank et al., 2016), prokaryotic and eukaryotic communities (e.g., Kahlert et al., 2022; Przytulska et al., 2017), among others. Changes affecting the landscape are, thus, directly linked to the functioning and health of the lakes and the communities that inhabit them, providing valuable information about the state of Arctic ecosystems (Saros et al., 2023).

Warming conditions and the multiple associated changes in the landscape, alone or combined, are expected to influence the degree of hydrological connectivity throughout the landscape (Wrona et al., 2016). Consequently, affecting the functioning of freshwater ecosystems reflected on the trophic state of water, the internal metabolic processes, and the interactions between microbial, phytoplankton and zooplankton communities, ultimately affecting larger organisms that depend on them (Wrona et al., 2006). Moreover, affecting human populations that rely on the ecosystem services that lakes provide to northern communities (Vincent et al., 2012; Figure 0.1).

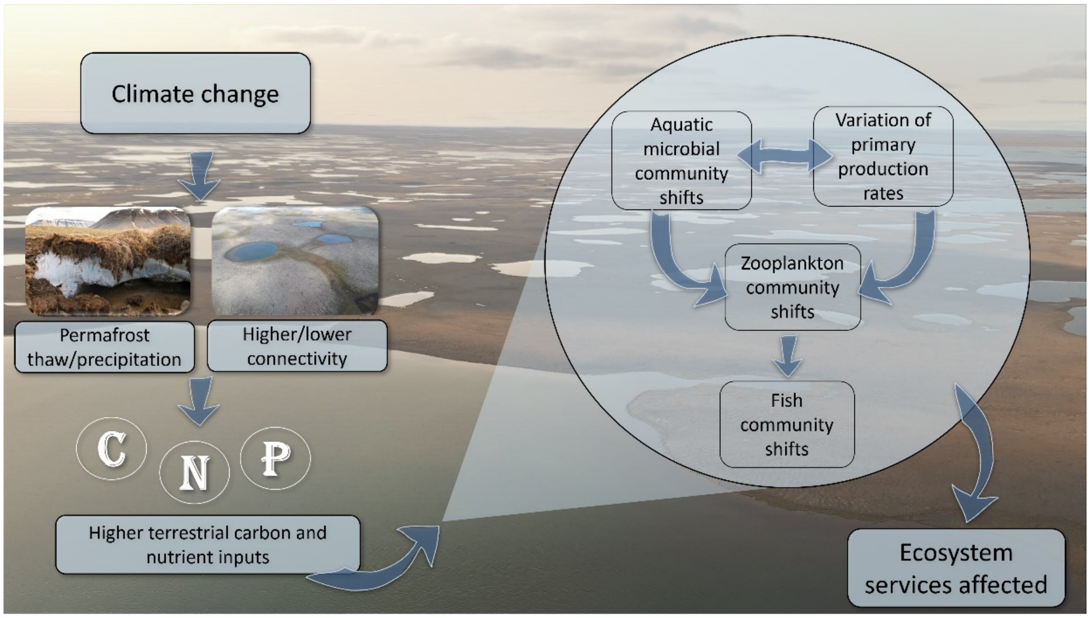

Figure 0. 1 Effects of climate change on terrestrial variables affecting aquatic ecosystems and the ecosystem services provided by lakes in the Arctic.

Northern indigenous communities are often strongly associated with lakes, which represent an important part of their culture, and are a predominant feature of the Arctic landscape (Downing et al., 2006). Indigenous communities rely on freshwater ecosystems for fishing, recreation, or as potable water sources (Stenekes et al., 2020), and are, thus, directly affected by changes happening in the landscape. Effects of climate change altering catchment characteristics, freshwater systems and species composition across the Arctic are already evidenced by researchers, but also by local communities (Knopp et al., 2022). Such processes are well documented and better understood in lower latitude lakes, however, the remoteness of Arctic ecosystems and associated limitations (e.g., reduced access by land, material transportation restrictions, elevated costs, etc.) still represent a barrier for researchers (Mallory et al., 2018). For the same reasons, limnological studies in the Arctic are often based on a single or a few lakes, and studies at a watershed scale are even less common. Thus, the available information of Arctic freshwater systems and the relationship with their catchment remains limited due to the large extent of unstudied territory, and most Arctic studies are concentrated in a few sites of similar characteristics (Metcalfe et al., 2018).

Furthermore, Arctic regions of low elevation, with low precipitation rates and low effect of permafrost degradation, like the Greiner Lake watershed that is the focus of this study, are often overlooked in the Arctic literature. Lakes in such regions may behave differently from other high latitude lakes due to the climatic conditions and the characteristics of the catchment (Bogard et al., 2019) leaving a knowledge gap that needs to be filled. The study of Arctic lakes and their relationship with their catchment provides valuable information about the state of the lakes, the aquatic communities living in them as well as the state and health of their surrounding environment. Understanding the present state and functioning of Arctic freshwater ecosystems is highly important to understand their participation in the carbon cycle and effects on a global scale. Current research in different regions of the Arctic will provide crucial base information for identifying local changes and planning future adaptation and mitigation programs for northern communities.

0.2 State of the science

0.2.1 Arctic lakes as sentinels of climate change

Lakes act as integrators of the landscape as they gather water and other materials from the watershed from headwaters to the downstream receiving lake (Vincent, 2018). However, in the Arctic they not only act as integrators, but also as sentinels of climate change as they more efficiently integrate and reflect the changes of the landscape provoked by the faster pace that the climate change affects the Arctic compared to other regions in the world (Adrian et al., 2009).

Regime shifts on Arctic lakes attributed to ongoing climate change show how responsive they are and the large amount of information they can provide in this matter (e.g., Huser et al., 2020; Quinlan et al., 2005; Smol et al., 2005). Changes in freshwater ecosystems can be evidenced in changing productivity, shifting biogeochemical cycles, and mixing regimes, among others (Wrona et al. 2016). Adrian et al. (2009) provide a list of key variables that allow to determine direct or indirect effects of climate change on lakes, that include physical (i.e., water temperature, water level, stratification, turbidity), chemical (i.e., dissolved organic carbon, oxygen, pH), and biological (i.e., relative species composition, primary productivity) properties. Many of the sentinel variables are analyzed in the frame of this project, giving a complete overview of the state of Arctic lakes in the studied watershed.

0.2.2 Hydrological connectivity

As lakes integrate water and materials throughout the landscape, assessing the structure of the watershed, and the interactions between lakes and their watersheds through measurements of hydrological connectivity, can provide important information to explain the physical, chemical and biological properties of lakes (Covino, 2017).

Although there are multiple definitions of hydrological connectivity (Ali & Roy, 2009), the ecological definition proposed by Pringle (2003) in an ecological context is adopted here, as:

> "…water-mediated transfer of matter, energy and/or organisms within or between elements of the hydrologic cycle"

This definition encompasses the physicochemical and biological elements, integrating the landscape with the lakes, but also the internal elements of a lake.

There are multiple ways of measuring hydrological connectivity proposed in the literature (Ali & Roy, 2009). A few of them are directly or indirectly addressed in this doctoral project, including: a) lake and stream metrics, such as distance between lakes, number of upstream lakes (Stachelek & Soranno, 2019); b) terrestrial-water metrics, such as sub-watershed or watershed size in relation to lake area (Fergus et al., 2017; Stachelek & Soranno, 2019); c) spatial connectivity, measured by the physical location of the lake in the watershed (Fergus et al., 2017); d) time-based connectivity, categorizing lakes as permanently isolated temporally connected, and always connected (Jones et al., 2017); e) biological connectivity, measuring connections based on the movement of organisms across the landscape (Smith et al., 2019).

0.2.3 Trophic state of Arctic lakes

The trophic state of a lake describes the amount of biological productivity it sustains. It is linked to nutrient levels, species composition and abundance, amount of toxins, water clarity, oxygen content and greenhouse gas emissions (Keva et al., 2021; Kortelainen et al., 2006). Characterization of the trophic state of Arctic lakes is necessary as water quality basic information and for understanding the biogeochemical processes happening within (Smith, 2003).

There are a few ways to asses trophic status of lentic systems, including total phosphorus (TP), chlorophyll *a* (Chl *a*) concentration and Secchi depth (Carlson, 1977). TP concentration is the most commonly used variable to characterize the trophic status as it is often a good predictor of algal biomass (Downing et al., 2001; Schindler et al., 1978). Carlson and Simpson (1996), developed a trophic state index that allows to classify lakes in four categories using TP concentration: oligotrophic (0-12 µg/L), mesotrophic (12-24 µg/L), eutrophic (24-96 µg/L) and hypereutrophic (>96 µg/L). Total nitrogen (TN) can also be used to calculate trophic state index in a modified version of Carlson and Simpson (1996) index for nitrogen-limited lakes (Kratzer & Brezonik, 1981). Arctic lakes often fall under the oligotrophic or ultraoligotrophic categories (Vincent et al., 2009), with low TP concentrations and low content in Chl *a*.

0.2.3.1 Drivers influencing trophic state of Arctic lakes

The content of nutrients in the water [i.e., Phosphorus (P) and Nitrogen (N)] that allow to determine the trophic state of a given lake, in low latitudes, is mostly determined by anthropogenic sources (Paerl, 2014), however, they are less common in Arctic regions. Besides punctual cases like Meretta Lake on Cornwallis Island (73°N) (Douglas & Smol, 2000), direct anthropogenic pressure is not significant enough to induce responses in Arctic aquatic ecosystems (Smol et al., 2005). The main drivers influencing the trophic state of Arctic lakes are nutrient concentration often associated with organic matter input to the water coming from the catchment (Bring et al., 2016; Wrona et al., 2016). Nutrients, in the Arctic landscape, are mainly determined by the type of underlying bedrock that can leach phosphorus (P) into the waterbodies (Van Soest et al., 2022). Thus, P concentration in the water can be increased by P leaching from P-rich rocks like alkali basalts, contrastingly, ultramafic rocks with less P content may have less effect on water composition (Porder & Ramachandran, 2013). In areas affected by permafrost degradation, organic-rich soils are mobilized allowing the input of higher amounts of nutrients to the water (Wauthy et al., 2018). Another known source of nutrients are large bird populations (Hargan et al., 2017) that modify the terrestrial landscape through intensive grazing and bringing a high load of nutrients through feces accumulation (Buij et al., 2017; Cadieux et al., 2005). Additionally, atmospheric deposition has greatly increased with industrial development related to the increasing population density in the northern hemisphere (Bergström & Jansson, 2006). It has also showed to be an important source of P and N for the Arctic landscape (Choudhary et al., 2016; Moiseenko & Bazova, 2024), adding to the sources collected by the catchment and accumulated in lakes.

With the ongoing climate change, increasing temperatures in the Arctic promote earlier bird migration towards the north (Canadian Wildlife Service Waterfowl Committee, 2020; Fox et al., 2010), higher rates of permafrost thaw, altering water flux and flow paths, and mobilizing minerals and nutrients trapped in the soil and the catchment (Reyes & Lougheed, 2015; Walvoord & Kurylyk, 2016). Although eutrophication in Arctic lakes is often associated to direct human impact, as is the case of sewage water discharge in Meretta Lake (Douglas & Smol, 2000), the abovementioned nutrient enrichment sources can also provoke eutrophication in Arctic lakes (Mariash et al., 2018b; Van Geest et al., 2007). While eutrophic Arctic lakes are rarely mentioned in the literature, a few studies documented high TP values indicating a eutrophic trophic state in lakes (e.g., Dranga et al., 2018; Wauthy & Rautio, 2020).

0.2.4 Lake metabolism in Arctic lakes

0.2.4.1 Definition of lake metabolism

The term lake metabolism refers to the balance between gross primary production (GPP) and ecosystem respiration (ER), giving as a result the net ecosystem production (NEP) as in equation 0.1 (Wetzel, 2001b).

$$NEP = GPP - ER \tag{0.1}$$

GPP in a lake is the result of planktonic, benthic and periphytic primary production converting inorganic materials with the help of radiation to produce biomass, while ER is the sum of autotrophic and heterotrophic respiration from all organisms within a lake (Wetzel, 2001a). The study of lake metabolism allows the understanding of the interactions of lakes with the surrounding watershed and the atmosphere, but also the internal dynamics of production and respiration that shape the participation of lakes in the local and global carbon cycle (Cole et al., 2007). The resulting balance, expressed as NEP indicates whether the ecosystem is net autotrophic, acting as net organic carbon producers (NEP > 0), or net heterotrophic (NEP < 0), acting as a site of net organic carbon mineralization (del Giorgio & Williams, 2005; Lovett et al., 2006).

0.2.4.2 Methods to estimate net ecosystem production

NEP can be estimated through different methods that allow to determine either GPP, ER or both that will consequently be used to calculate NEP. There are a few commonly used assessment methods described in the literature and they are summarized below.

GPP using bottle incubations use ^{14}C labelled inorganic molecules such as HCO_3 as carbon source incorporated by photosynthetic organisms. The technique, introduced by Steemann Nielsen (1952), spikes a water sample with a known concentration of the labelled molecule which is then incubated exposed to light to allow incorporation. Finally, the incorporated carbon is quantified in the phytoplankton cells, giving an estimate of the primary production per volume and time unit. ER can also be assessed through the bottle incubation technique, but in this case by measuring the consumption of DO in dark bottles using chemical indicators of oxygen to be quantified with titration (Carignan et al., 1998).

The free water method measuring DO using submerged probes was first proposed for metabolism measurements in lentic systems (Odum, 1956), however, as they allow for large data to be collected in time and space, they were adopted for measurements in lotic systems as well (Staehr et al., 2010a). The technique follows changes in DO in the water reflecting the photosynthetic production and respiration of the ecosystem, that are integrated in a mass balance equation including exchanges with the atmosphere (Staehr et al., 2010a).

Both the bottle incubation and the free water methods allow to estimate benthic production to be included in the metabolic balance, however they require additional incubation or measurements to be integrated in the study (Van De Bogert et al., 2007), failing to include this important compartment of lakes may result in unrealistic metabolic values, especially in lakes with predominantly benthic primary production (Vadeboncoeur et al., 2002).

The measurement of the partial pressure of CO_2 (pCO_2) is another method that follows the changes in pCO_2 as an indicator of ecosystem respiration. This method determines if lakes are supersaturated or undersaturated in CO_2 compared to the atmosphere, and thus, allows to see if respiration exceeds production or if production exceeds respiration, respectively. It can be directly measured either using submerged fluorescence sensors (Atamanchuk et al., 2014) or through gas chromatography after equilibration of the water sample with atmospheric air (e.g., Prėskienis et al., 2021). This latter method is preferred especially in sites of net heterotrophic production for a more accurate assessment of respiration rates (Ask et al., 2012).

The oxygen isotope technique proposed by Bogard et al. (2017) uses $\delta^{18}O$ content in DO and in water ($\delta^{18}O$-O_2, $\delta^{18}O$-H_2O) in samples from surface water, associated with DO concentration and saturation. This approach assumes isotopic equilibrium of DO in surface water and includes atomic fractionation due to gas solubility effects, photosynthesis and exchange between air and water. The results are submitted to mass balance equations including the gas exchange and fractionation factors, producing values for both GPP and ER. Although there are some limitations in this as in the other known methods (Bogard et al., 2017), this technique allows the study of larger number of lakes with a single sample per lake, due to the easy sample collection, especially in remote areas as in the Arctic (Bogard et al., 2019).

0.2.4.3 Drivers of lake metabolism

Lake metabolism is determined by multiple factors that influence directly or indirectly GPP and R rates. However, two major factors regulate GPP by promoting or reducing photosynthesis and they are light availability and nutrients (Karlsson et al., 2009). On the other hand, respiration depends on several factors such as temperature (Gudasz et al., 2010), availability of organic matter present as dissolved organic carbon (DOC) from external (Lapierre et al., 2013) or internal (Bogard et al., 2019) sources and trophic state of the lakes (del Giorgio & Peters, 1994). However, different lakes show different patterns with the variation of the interaction between the abovementioned variables, thus, there is no one rule to determine metabolic patterns for all lakes. The metabolic state of lakes will vary with latitude (Vadeboncoeur et al., 2003), land use, type and size of surrounding watershed (Lapierre et al., 2015), lake morphometry (Staehr et al., 2012), and hydrological connectivity (Johnston et al., 2020). As lake metabolism is so strongly linked to the changes in the surrounding environment, the importance of studying lakes at a watershed scale becomes more important, especially for understanding ecosystem responses to climatic variations (Jones et al., 2017).

0.2.5 Carbon transfer in freshwater Arctic food webs

0.2.5.1 Food web structure in Arctic lakes

Arctic lakes are characterized by rather simple food webs (Kling et al., 1992), mostly constrained by the low trophic state, characteristic of high latitude lakes, low temperatures, extreme variations in solar radiation, and hydrological connectivity (Hershey et al., 1999; Rautio et al., 2009). The structure of the food web is composed of primary pelagic and benthic producers, primary pelagic and benthic consumers (i.e., zooplankton and zoobenthos), and, in cases, secondary consumers (i.e., fish; Grosbois et al., 2022). The presence of fish and the general structure of food webs of Arctic lakes is determined, to a greater extent, by the degree of hydrological connectivity and lake size (Laske et al., 2016). Lakes connected through rivers allow the passage of fish coming from the sea or from adjacent lakes and is important for species that need a refuge for overwintering (Christoffersen et al., 2009; Eloranta et al., 2015). Consequently, the presence of fish has a top-down control on the rest of the food web, regulating the composition and abundance of zooplankton groups that affect the phytoplankton community in their turn (Figure 0.2a; Christoffersen et al., 2009). Fish presence exerts pressure on zooplankton communities altering the proportions of copepods versus cladocerans. In lakes where fish are present, large zooplankton species (e.g., cladocerans) are often absent or are only present in small numbers (Blackburn-Desbiens et al., 2023). The opposite is observed in fishless lakes, where microbial and phytoplankton communities regulate zooplankton production and abundance (Hobbie et al., 2000). Zooplankton in this type of lakes can reach larger size and be more abundant, also representing the highest level of the food web (Figrue 0.2b; Blackburn-Desbiens et al., 2023; Rautio et al., 2009).

The microbial component of food webs is less studied or at least less integrated in the Arctic food web literature, where very often microorganisms are left aside or studied separately. However, from an energetic point of view, the role of heterotroph and mixotroph protists is highly important in the transfer of carbon along the food web (Mitra et al., 2014; Wickham & Wimmer, 2019) as they upgrade carbon from picoplankton to be transferred to higher trophic levels (Bec et al., 2006).

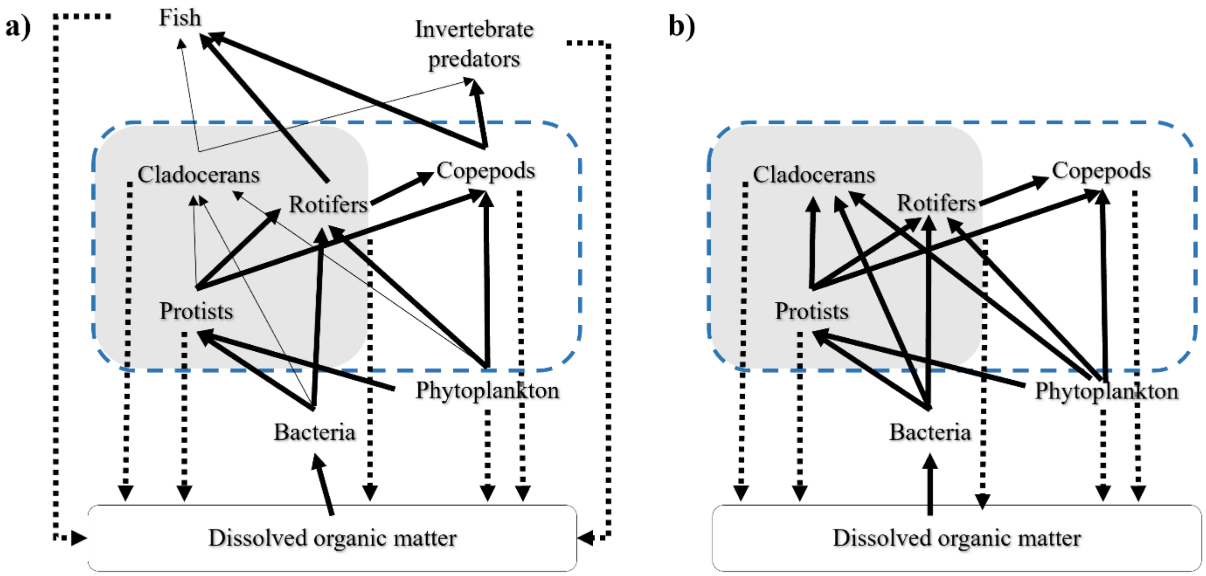

Figure 0. 2 Food web representation of a) Arctic lakes with fish and b) Arctic lakes without fish. Figures adapted from Christoffersen et al. (2009) and modified based on Brandl (2005) and Bégin and Vincent (2017). Dashed rectangles are herbivores. Organisms over the shaded area represent bacterivorous groups. Solid arrows represent energy flux. Dotted arrows indicate the release of dissolved organic matter.

0.2.5.2 Essential fatty acids in the food web

Fatty acids are naturally occurring molecules that are important structural and functional parts of the cells of all living organisms. They are building blocks of cellular membranes and they serve as food reserve that can be used as source of energy when broken down (Alberts et al., 2014). Polyunsaturated fatty acids (PUFA) are a subgroup of fatty acids, they have two or more double bonds between their carbon atoms that allow fluidity of the molecules and of the structures they form (Alberts et al., 2014). PUFA are highly important for the growth and reproduction of organisms and is why they are called essential fatty acids for consumers. In general, consumers cannot synthesize PUFA or at least not in enough quantities to supply their physiological requirements (Desvilettes & Bec, 2009). Phytoplankton that are the sources of PUFA by excellence, they synthesize PUFA *de novo*, and are, thus, responsible of supporting higher levels of the food web (Galloway et al., 2014; Iverson, 2009). PUFA from primary producers are transferred to herbivores that consume them directly or indirectly to secondary consumers as part of their integrated diets (Persson & Vrede, 2006). Although most primary producers synthesize some sort of polyunsaturated fatty acids, a few taxonomic groups in the plankton are recognized for their higher content and better quality of PUFA. Cryptophyceae, Bacillariophyceae, Euglenophycea, Raphidophyceae (Taipale et al., 2013), and Dinophyceae (Ahlgren et al., 1992) are known as high quality PUFA producers, although variations are observed among species, and across habitats (Peltomaa et al., 2019). Thus, the presence of specific high-quality phytoplankton in freshwater food webs proved to be of high importance for higher trophic levels (i.e., zooplankton and fish). Phytoplankton rich in PUFA, but more specifically eicosapentanoic acid (EPA; 20:5n3) and docosahexanoic acid (DHA; 22:6n3), promote high PUFA content in zooplankton. Moreover, they promote the highest rates of growth and reproduction of zooplankton as observed in previous studies (Brett & Müller-Navarra, 1997).

Fatty acids are an important adaptation to low temperatures for organisms living in cold environments and as energy storage molecules under limiting conditions (Yu et al., 2009). It is not surprising then, that algae and zooplankton in high latitudes have higher PUFA content compared to lower latitudes (Hessen & Leu, 2006), and their presence is important for the survival of long winter periods. As zooplankton obtain essential fatty acids from their pray, zooplankton survival during winter relies significantly on the content of PUFA in phytoplankton (Grosbois et al., 2017). Similarly, in lakes where fish are present, zooplankton rich in PUFA are important for fish survival through winter (Eloranta et al., 2013).

As global warming progresses, increasing temperatures altering light availability, tropic state, and water temperature, among other disruptions in the environment, may affect the ability of planktonic organisms to produce and store fatty acids with the same efficiency as they do under colder conditions or low light conditions experienced during the ice covered and transitional season (Adlerstein et al., 1997; Hébert et al., 2021). Subsequently, the structure of food webs may be altered along with the content of PUFA in each trophic level as shown in a space-for-time study in lakes in northern Finland (Keva et al., 2021). Keva et al. (2021) showed that with increasing trophic state not only the phytoplankton composition changed towards cyanobacteria dominated communities, but the PUFA content in zooplankton decreased greatly.

0.2.5.3 Tracing carbon transfer in food webs

Tracing the sources of organic matter supporting lake food webs can be challenging, as it is not always easy to determine who eats who, especially in the lower levels of the food web. The most common tools to study food webs are fatty acids and stable isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$), as markers of both the putative resources and consumers. They both allow to reconstruct the pathways through which carbon and other organic resources are assimilated (Iverson, 2009; Middelburg, 2014). Stable isotopes similarly vary between organisms depending on the source and number of previous trophic transfers. Both $\delta^{13}C$ and $\delta^{15}N$ change at a predictable and known rate when trophically transferred. With $\delta^{13}C$ in consumers resembling more to the one in their diet, but $\delta^{15}N$ increasing with increasing trophic level (Traugott et al., 2013). The most common isotopes to be studied in ecology are carbon and nitrogen, but hydrogen, oxygen, and sulfur are also used in some studies (del Rio et al., 2009; Gannes et al., 1998). Although the use of stable isotopes allows the reconstruction of food webs and can help differentiate between herbivores and carnivores, it has certain limitations in resolution at lower trophic levels.

In that case, specific fatty acids from described groups of algae and bacteria, can help identifying the presence of certain planktonic and groups (Ahlgren et al., 1992; de Carvalho & Caramujo, 2018). Fatty acids usually do not change when they are transferred from source to consumer, which is why they can be used as algal biomarkers in trophic transfer studies along the food web (Dalsgaard et al., 2003; Taipale et al., 2013). More recently, the use of compound specific isotopes from fatty acids has increased the precision at determining food sources as $\delta^{2}H$ and $\delta^{13}C$ are highly preserved through trophic transfer (Pilecky et al., 2021). Compound-specific $\delta^{2}H$ in combination with compound-specific $\delta^{13}C$ produce better results in tracing fatty acid sources in the food web (Pilecky et al., 2022). However, to accurately determine the putative algal food sources of zooplankton, the composition of the phytoplankton needs to be determined. In the literature this is often achieved through microscopic identification and enumeration (e.g., Kankaala et al., 2010). Although some studies have bypassed microscopy, opting for Bayesian mixing models using libraries of fatty acid signatures from identified algae (Galloway et al., 2015; Strandberg et al., 2015), the results may sometimes be unrealistic or contradictory. If the phytoplankton community is unknown and libraries are elaborated with only a number of species that are representative of one environment, it is hard to extrapolate the data for other ecosystems as many assumptions have to be made. Some assumptions include that there is only a few potential food sources for zooplankton for all the tested lakes, also that the fatty acids of described phytoplankton in the available library are unique to each algal group. This reduces the probability of finding interactions among photosynthetic organisms, mixotrophs and heterotrophs as potential fatty acid sources. Overlooking some of the less known groups that may have a function in the food web may lead to unexpected or even wrong results. Keva et al. (2023), for instance, used fatty acid profile libraries from a different community and found that dinoflagellates were an important source of PUFA for zooplankton, while the previous study stated that dinoflagellates were low quality algae (Galloway et al., 2015). To avoid such issues, other studies propose the combination of various techniques that could be more precise at identifying phytoplankton groups, using fatty acids, sterols, and carotenoid profiles of algae (Peltomaa et al., 2023). Even though Peltomaa et al. (2023) obtained somewhat good results to detect large algal groups, the use of these techniques to determine the structure of the phytoplankton may still need validation.

In actuality, the most employed and fast-growing technique for detection and identification of small organisms in the order of pico- and nanoplankton, which often dominate the phytoplankton community, are molecular based techniques based on 18S DNA and 16S DNA sequencing.

Although, as with all techniques, it has some caveats, notably the lack of full taxonomical databases for organism identification. However, the available information is constantly improving as new species are identified and included in the databases (e.g., Guillou et al., 2013). This technique, coupled with fatty acids and stable isotopes, may represent an optimal combination for studying food webs in aquatic ecosystems, spanning from bacteria to fish.

0.3 Objectives, hypotheses, and structure

The overarching objective of this doctoral work is to determine how various aspects of hydrological connectivity within an arid, low elevation Arctic watershed contribute to defining the state of the lakes, their planktonic communities, and the related biogeochemical processes and food webs across the watershed. The results of this study will contribute to the growing literature on freshwater ecosystems of an understudied Arctic region, providing data gathered from 35 lakes. Current information about different regions of the Arctic biome will provide the ground for understanding changes in this vulnerable region as climate warming progresses. To achieve the general objective, this project was divided into three chapters written in the form of scientific articles (chapters 1, 2 and 3), each with objectives describing different features and processes in the set of lakes in the watershed. The specific objectives for three chapters are described below.

Chapter 1. Trophic state

In this chapter the trophic state of the lakes were described using Carlson's (1977) trophic state index based on TP and Chl *a* with the aim to report the presence of a eutrophic Arctic lake (ERA5) from the Greiner Lake watershed while describing the general state of the watershed. The phytoplankton community was quantified to assess how the trophic state and the relationship with hydrological connectivity affect the phytoplankton composition in Arctic lakes. Lakes in this study were compared to lakes in the published literature, bringing attention to the presence of eutrophic lakes without direct human influence in the Arctic landscape. The study further highlighted the possible effects of ongoing global warming on the trophic state of shallow isolated lakes that are a major component of Arctic landscapes.

Chapter 2. Metabolism

This chapter explores the metabolic state of lakes in the Greiner Lake watershed, with emphasis on the effect of hydrological connectivity on the water composition that determined the processes within the lakes. Lake metabolism was assessed using stable isotopes from water and dissolved oxygen ($\delta^{18}O$-H_2O and $\delta^{18}O$-O_2), [^{14}C]-HCO_3 incorporation in pelagic and benthic compartments and CO_2 concentration in the water as means to understand the biogeochemical processes shaping the metabolic state of the lakes. The results showed that most lakes had a net autotrophic metabolism with headwater lakes showing higher values of NEP and midstream and downstream lakes being closer to metabolic equilibrium. Lake metabolism was associated with the chemical composition of the water as headwater lakes had higher concentration of carbon and nutrients as a result of higher evapoconcentration rates. In contrast, downstream lakes, that had larger water volume, had lower concentration of solutes. However, the composition of carbon, especially in headwater lakes, was of autochthonous production and little allochthonous input was detected, indicating an important link between internal carbon and nutrient recycling with lake metabolism. This study showed how lakes in low elevation and arid landscapes have a different metabolism from lakes elsewhere in the Arctic literature, emphasizing the importance of shallow headwater lakes as sites of net organic production and acting as potential sinks of CO_2.

Chapter 3. Carbon transfer

The third chapter focuses on the carbon transfer at the base of the food web along a depth gradient of 35 lakes. First, stable isotopes ($\delta^{13}C$ and $\delta^{15}N$) were used to determine the major food source for zooplankton. The phytoplankton community composition was then determined through 18S DNA sequencing and coupled with the PUFA composition of the zooplankton to establish the most important phytoplankton groups providing PUFA for the food web. Stable isotopes indicated that zooplankton in all lakes depended mostly on phytoplankton as a food source. However, zooplankton in shallow lakes showed a mixed diet between phytoplankton and benthic mats that are highly productive and easily resuspended by the wind. Lake depth was highly correlated with hydrological connectivity, shaping the chemical composition of the water with a direct effect on the composition of the microbial eukaryotic community. Higher PUFA contents were observed in zooplankton of deep, more oligotrophic lakes that had higher proportion of dinoflagellates compared to the shallowest, less oligotrophic lakes. This chapter links with the first and second chapters highlighting the importance of hydrological connectivity for the trophic state and phytoplankton composition of shallow Arctic lakes shaping the available carbon sources that sustain the aquatic food web.

0.4 Methodological approach and study sites

This doctoral project concentrates on data from 35 lakes of the Greiner Lake watershed. The watershed is located on southern Victoria Island, Nunavut (Figure 0.3a and b). Greiner Lake (69° 10’ 35.72" N, 104° 55' 54.87" W), located near the hamlet of Cambridge Bay, Nunavut has a significant value for the local Ikaluktutiak Inuit community. Greiner Lake is an important part of the community’s identity because of the ecosystem services it provides, such as drinkable water, recreational areas, aesthetic landscape, and food. Greiner Lake is also important in the context of the watershed as it receives water from over a thousand upstream lakes (Figure 0.3d), connecting a landscape area of 161859 ha. The lake is connected to the Arctic Ocean by an outlet that allows the migration of fish during the ice-free season.

Sampling was carried out during the open water season, in August 2018 and 2019, with additional supporting samples taken in 2022. The lakes were accessed by truck or all-terrain vehicles or by helicopter when they were not accessible by road. All samples were immediately transported to the Canadian High Arctic Research Station (CHARS; Figure 0.3c), where they were filtered, preserved, frozen, sorted and labeled, depending on the nature of sample. Details on the samples and the analytical methods employed are detailed in the methods section of each chapter.

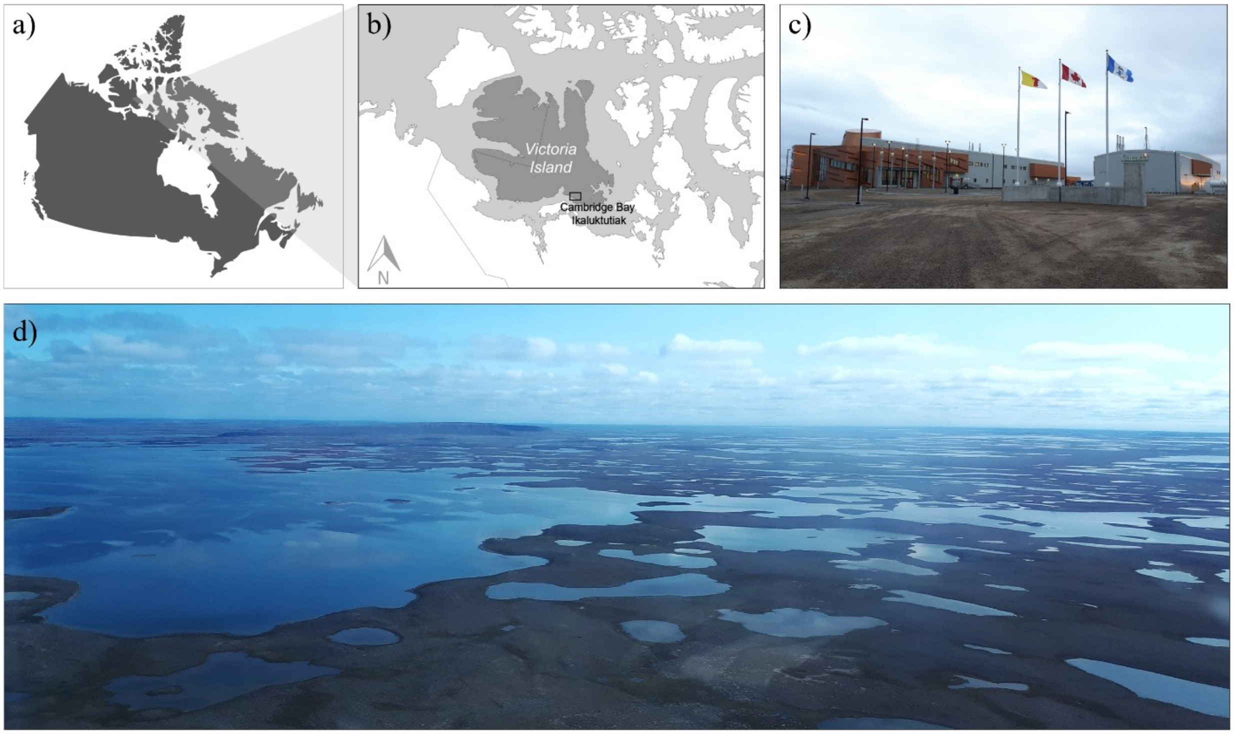

Figure 0. 3 a) Map of Canada indicating the position of Victoria Island in the Canadian Arctic Archipelago. b) Victoria Island indicating the position of Cambridge Bay (Ikaluktuttiak) in the south of the island. c) The Canadian High Arctic Research Station (CHARS). d) Aerial of the Greiner Lake watershed, showing the low elevation of the landscape. Greiner Lake is on the left and Mount Pelly in the far background.

CHAPTER 1 TROPHIC STATE

Evidence of eutrophication in Arctic lakes

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1.1 Abstract

Lakes and ponds are dominant components of Arctic landscapes and provide food and water for northern communities. In the Greiner Lake watershed, in Cambridge Bay (Nunavut, Canada), water bodies are small (84% < 5 ha) and shallow (99% <4 m). Such characteristics make them vulnerable to eutrophication as temperatures rise and nutrient concentrations from the greening landscape increase. Here, we investigated and compared 35 lakes and ponds in the Greiner watershed in August 2018 and 2019 to determine their current trophic states based on their chemical composition and phytoplankton communities. The ponds had higher trophic status than the lakes, but overall, most sites were oligotrophic. Lake ERA5, located upstream of any direct human influence was classified as eutrophic due to high total phosphorus (32.3 $\mu g\ L^{-1}$) and a high proportion of Cyanobacteria (42.9% of total phytoplankton biovolume). Satellite imagery suggests the lake may have been eutrophic for the last 30 years. We hypothesize that the coupled effects of catchment characteristics and elevated local snow accumulation patterns promote higher nutrient leaching rates from the soils. We recommend further analysis and monitoring as eutrophication could become more widespread with ongoing climate change and the associated increases in temperature, precipitation, and catchment-lake coupling.

1.2 Introduction

Lakes and ponds are a striking component of many Arctic landscapes and provide migratory nesting birds, resident animals and humans with food and freshwater. The water bodies experience strong seasonal fluctuations, from complete ice cover, with low or no light and hypoxic conditions during much of the year to open water, water column mixing, full oxygenation, air temperatures above freezing and 24-hour light cycles during the brief summer. Their limnological characteristics and those of the surrounding landscapes make them sensitive to small changes in the environment and within the context of Arctic freshwater science they are typically viewed as "sentinels of climate change" (Vincent et al., 2009).

Arctic lakes are impacted by climate change that is affecting the Arctic twice as fast as other areas in the world. Increasing temperatures have had measurable effects on many different levels of Arctic ecosystems, from earlier ice breakup (Cooley et al., 2020; Šmejkalová et al., 2016; Vincent et al., 2011) through increases in vegetation cover (Campbell et al., 2020) to changes in bird populations (Menu et al., 2002). With temperature-driven permafrost thaw, changes in hydrologic connectivity leading to erosion are also becoming more evident (Liljedahl et al., 2016), along with increasing evaporation/precipitation ratios leading to higher ion concentrations or even desiccation of shallow water bodies (Smol & Douglas, 2007). The resulting mineral mobilization increases phosphorus (P) input to freshwaters, especially in regions with naturally high P concentrations in the bedrock and soil (Vonk et al., 2015). All these changes have an effect on freshwater communities, altering plankton diversity and production (Wrona et al., 2016). An additional potential consequence of warming is the increasing prevalence of phytoplankton groups, such as cyanobacteria, that prefer warmer temperatures and that have already been reported to respond to climate change in subarctic ponds (Przytulska et al., 2017).

Arctic lakes are typically oligotrophic, or even ultraoligotrophic, (Hamilton et al., 2001; Michelutti et al., 2002) and no cyanobacteria blooms are known to occur in lakes above the Arctic Circle. In fact, the highest latitude in Canada, where an algal bloom has been mentioned in the literature is Great Slave Lake ~60°N (Pick, 2016). With the exception of eutrophication caused by ancient whaling residues (Douglas et al. 2004), sewage (Rigler, 1972, 1974), and more recently by increased geese and seabird populations (Hessen et al., 2017; Jensen et al., 2019; Michelutti et al., 2009), eutrophic lakes are rarely mentioned in the Arctic scientific literature. Higher temperatures and increased weathering and leaching rates may, however, push the lakes across the threshold above which eutrophication would be triggered. Out of 1280 analyzed Canadian Arctic lakes and ponds, about 8% can be classified eutrophic based on their phosphorus (P) content using Carlson's Trophic State Index (Carlson, 1977; Dranga et al., 2018).

The rapid environmental changes occurring in the Arctic make it imperative to gather more information and better understand high latitude lake properties and their potential responses to climate change, which are largely unknown. Here, we describe the current trophic state of 35 water bodies in the Greiner Lake watershed, Victoria Island, Nunavut. We separated the water bodies into lakes and ponds based on their size, which affects their resilience to external nutrient inputs, and the presence or absence of fish, to account for differences in trophic state that may be associated with different food web structures and hence algal biomass (Rautio & Vincent, 2006). In addition to measuring nutrients and standard limnological parameters, we characterized the dominant phytoplankton groups, in particular, Cyanobacteria, and measured bacterial production as a proxy of decomposition that would make organic P more available to phytoplankton (Ger et al., 2014; Zhao et al., 2012), providing another indicator for eutrophication. We report on a specific eutrophic lake that was found amid oligotrophic lakes in the same watershed. The broader significance of the study is the contribution of contextual data on the current limnological state of freshwater ecosystems in the Arctic. This study draws attention to the importance of local differences in northern catchment-lake connections and is a contribution to the project Terrestrial Multidisciplinary distributed Observatories for the Study of Arctic Connections (T-MOSAiC).

1.3 Materials and methods

1.3.1 Study site

The Greiner Lake watershed is located on south Victoria Island (69° 10’ 35.72" N, 104° 55' 54.87" W), Nunavut, contains an estimated 6280 lakes and ponds and covers nearly 1500 km^2. The watershed is a source of both fish and potable water for the nearby Hamlet of Cambridge Bay, the fifth largest Inuit community in Nunavut with 1766 habitants in 2020 (Figure 1.1a). The watershed is also currently the focus of wider ecosystem change studies by the Canadian scientific community in conjunction with the Canadian High Arctic Research Station (CHARS).

Most of the lakes and ponds in the watershed are small (84% < 5 ha) and shallow (99% < 4 m). The larger lakes are always connected to the main watershed system and typically support fish populations consisting of varying combinations of Arctic Charr (*Salvelinus alpinus*), Lake Trout (*S. namaycush*), Lake Whitefish (*Coregonous clupeaformis*), Least Cisco (*C. sardinella*) and Nine-spine Stickleback (*Pungitius pungitius*). In contrast, ponds are smaller and shallower and typically isolated systems. Thus, following Rautio et al. (2011), ponds were classified here as fishless water bodies, disconnected from other water bodies at the time of sampling, with an average depth < 1 m and smaller than 10 ha in surface area.

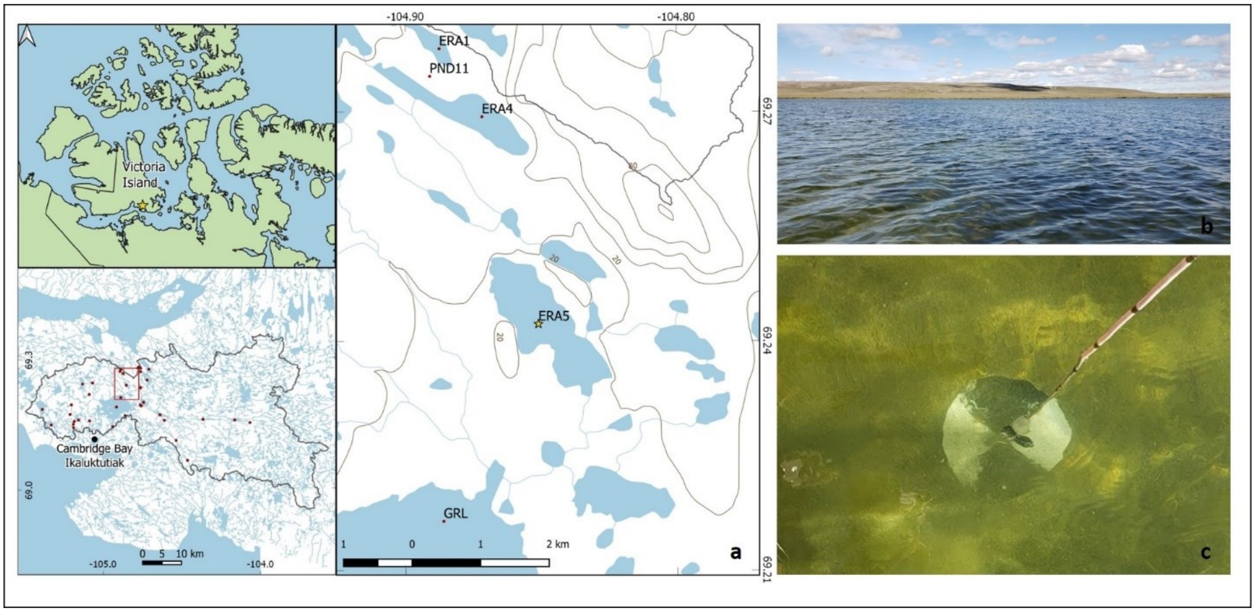

Figure 1. 1 a) Map of the Greiner Lake watershed, Victoria Island, Nunavut. Upper left panel shows Victoria Island with respect to the Canadian Arctic Archipelago. Lower left panel denotes the 35 sampled lakes and ponds (red dots). Right panel enlarges the red box outlined in the lower left panel and shows the main study site (ERA5) with Greiner Lake in the lower left corner. Created with Q-GIS 3.14, based on Landsat 8 OLI imagery courtesy of the U.S. Geological Survey (2020), Canada administrative limits (Natural Resources Canada, 2020a), Canada elevation data (Natural Resources Canada, 2020b) and in situ GPS data. b) View of lake ERA5 in July 2020. c) Green coloured water in the middle of lake ERA5.

1.3.2 Sampling and analyses

Single water and plankton samples were collected using a portable inflatable boat from 23 lakes and from the shore of 12 ponds in August 2018 and 2019. Lakes Greiner (GRL), 1ST, 2ND, ERA1, ERA4 and CBL5 were sampled in both years. Temperature, oxygen and conductivity profiles were measured *in situ* using a Ruskin RBR Concerto logger. Depth was measured using a depth sounder (Hawkeye DT1H) in both lakes and ponds. Water was collected from a single sub-surface depth in the ponds and up to five depths in lakes, using a 2–L Limnos closing water sampler (Limnos, Poland). Multiple casts were mixed in a clean 20 L bucket to make one composite sample. The collected water was immediately sub-sampled for Total Phosphorus (TP) and Total Nitrogen (TN) in individual acid-washed glass bottles. Two other subsamples were also filtered through a 0.45 µm syringe filter for Total Dissolved Phosphorus (TDP) and Dissolved Organic Carbon (DOC) and similarly stored in acid-washed glass bottles. Water for phytoplankton analysis was collected in 125–ml, Nalgene bottles and preserved with 0.5 ml of 5% Lugol's solution. The remaining water was transferred to 4–L Nalgene bottles placed in a "cooler" and brought to the laboratory at CHARS by helicopter or all-terrain vehicle (ATV) for Grenier Lake and close by lakes and ponds. Back at the laboratory, three replicates of 500 mL were immediately filtered through pre-combusted Whatman GF/F filters for chlorophyll *a* (Chl *a*) and stored frozen for later extraction. Bacterial production (BP) was measured immediately upon return from sampling using leucine incorporation following methods described in Kirchman (2001). Briefly, triplicate vials of 1.2 ml of unfiltered water were spiked with [^{3}H]-leucine (30 nM final concentration) and incubated for 3 hours at 10 ±2°C based on *in situ* measured temperatures (Table 1.1). Production after incubation was stopped using Trichloroacetic Acid (TCA, 50%). Two control vials with TCA were additionally prepared. Lake water and [^{3}H]-leucine were added to the TCA solution allowing measures and subtraction of passive absorption of leucine by the bacteria. All vials were preserved at -20°C until scintillation counting (see below).

Table 1. 1 Limnological characteristics of lakes, ponds and Lake ERA5. Area is the range of category for surface area of the pond or lake. Other values are mean ± standard deviation of 23 lakes and 12 ponds. Chlorophyll a (Chl a), Total nitrogen (TN), Total phosphorus (TP), Total dissolved phosphorus (TDP), Dissolved organic carbon (DOC).

	Unit	Lakes	Ponds	ERA5
Area	ha	4.31 - 3873.72	0.07 - 7.31	141.32
Depth	m	8.5 ± 7.6	0.5 ± 0.1	1.2
Chl a	µg L^{-1}	1.86 ± 1.08	2.30 ± 2.22	4.29
Temperature	°C	10.0 ± 1.0	10.0 ± 2.1	8.7
Conductivity	µS cm^{-1}	378.0 ± 185.3	549.3 ± 250.6	682.7
TN	µg L^{-1}	425.8 ± 163.7	1128.8 ± 216.4	940.0
TP	µg L^{-1}	8.4 ± 5.5	10.4 ± 2.6	32.3
TDP	µg L^{-1}	5.8 ± 1.3	8.4 ± 1.7	9.8
DOC	mg L^{-1}	5.0 ± 1.6	16.0 ± 2.8	9.9
Bacterial Production	µg C L^{-1} d^{-1}	31.7 ± 19.8	48.2 ± 31.6	112.1
Total phytoplankton biovolume	mm^3 L^{-1}	0.65 ± 0.61	1.11 ± 1.91	0.59
Chlorophyta biovolume	mm^3 L^{-1}	0.04 ± 0.04	0.12 ± 0.14	0.19
Cyanobacteria biovolume	mm^3 L^{-1}	0.02 ± 0.05	0.04 ± 0.09	0.25

TP, TDP, TN and DOC were analyzed by Environment and Climate Change Canada at the Burlington-National Laboratory for Environmental Testing following internal protocols (Environment Canada, 2019). Chl *a* samples were extracted in 90% ethanol and analyzed spectrofluorometrically following Nush (1980). Bacterial production samples were concentrated by centrifugation at 12000 rpm to pellet the bacteria. The bacteria pellet was re-suspended in a 1 ml scintillation cocktail and let sit for 24 hours. Radioactivity was measured using a Perkin Elmer Tri-Carb 2910 scintillation counter. Phytoplankton were enumerated (counts) by microscopy by Biologica Environmental Services Ltd. Depending on the Chl *a* concentration of each lake, sub-samples from 3 (for highly concentrated samples) to 100 ml were analyzed after 24 to 48 hours sedimentation in Utermöhl chambers (Lund et al., 1958). Counting was done using a Zeiss Axio Vert A.1 inverted phase contrast microscope at 400x magnification. All algal cells were counted in a series of random fields of view until a minimum of 300 algal units were enumerated (Grace

Analytical Lab, 1994). Biovolume calculations were performed by measuring at least 10 cells of each taxon and applying the standard geometric formula with the best fit to the shape of the cell (Hillebrand et al., 1999). Finally, Landsat 5TM and 8 OLI imagery, courtesy of (U.S. Geological Survey, 2020), was used to compare the colour of ERA5 and adjacent lakes from 1989 to 2019. Satellite data were processed using Q-GIS 3.14. Each band was converted into apparent reflectance values and atmospherically corrected, re-projected into the NAD83 UTM Zone 13N coordinates system and displayed in RGB composition using the corresponding bands (Jensen, 2016).

1.3.3 Data analyses

The Trophic State Index (TSI) classifies lakes according to their trophic state, using Chl *a*, Secchi depth or TP values (Carlson, 1977). Lakes can be classified into 5 different categories: ultra-oligotrophic, oligotrophic, mesotrophic, eutrophic and hypereutrophic (Carlson & Simpson, 1996). The TSI for all lakes was calculated using equations 1.1 and 1.2 as proposed by Carlson (1977) using Chl *a* and TP values, respectively.

$$TSI(Chl\ a) = 10\left(6 - \frac{2.04 - 0.68 \ln Chl\ a}{\ln 2}\right) \tag{1.1}$$

$$TSI(TP) = 10\left(6 - \frac{\ln \frac{48}{TP}}{\ln 2}\right) \tag{1.2}$$

Phytoplankton community abundance structures (based on Bray-Curtis similarity) were compared between ponds and lakes using permutational multivariate analysis of variance (PERMANOVA) (Anderson et al., 2008) run with 999 permutations. Prior to analyses the data sets were reduced from 109 to 44 taxa to retain species that contributed at least 5% of the total abundance found in a lake or pond and all data were square root transformed using shade plot methods (Clarke et al., 2014). PND4 was excluded from the analyses as it contained only one taxon, which made it an outlier in the analyses. Multivariate analyses and ordinations were run using PRIMER+PERMANOVA v.7 (Anderson et al., 2008; Clarke & Gorley, 2015).

1.4 Results

A clear difference between lakes and ponds could be seen in the field, as lakes were well connected via rivers and streams. Ponds, on the other hand, were disconnected, smaller and had abundant large-sized zooplankton visible to the naked eye, which indicated a lack of significant vertebrate (e.g. fish) predation. The ponds also had an overall higher trophic status compared to the lakes, with 20% higher mean Chl *a* and TP, 30% higher TDP, 62% higher TN, 70% higher DOC and a 40 % higher phytoplankton biovolume (Table 1.1). However, of the 35 lakes and ponds studied, TP values were higher in one lake (ERA5) compared to any of the ponds (32.3 $\mu g\ L^{-1}$). Lake ERA5 (Figure 1.1b and 1.1c) also had the highest values for TDP (9.8 $\mu g\ L^{-1}$), Chl *a* (4.29 ± 1.18 $\mu g\ L^{-1}$), TN (940 $\mu g\ L^{-1}$) and DOC (9.9 $mg\ L^{-1}$) among the studied lakes (Table 1.1).

The TSI calculated for TP indicated that most lakes and ponds were oligotrophic or ultraoligotrophic. Only three ponds were mesotrophic (PND3, PND8 and PND10) (Figure 1.2a). However, lake ERA5 was classified as eutrophic based on its high TP value. Using the TSI for Chl *a*, most lakes and ponds were classified as oligotrophic, but some lakes (ERA5, CBL1, CBL2) and ponds (PND10, PND11, PND18) were classified as mesotrophic. Based on Chl *a* there was a single eutrophic pond (PND4), although it classified as oligotrophic according to its P concentration (Figure 1.2a).

Bacterial production values in lakes averaged 31.7 ± 19.8 μg C L^{-1} d^{-1} and in ponds 48.2 ± 31.6 μg C L^{-1} d^{-1} (Table 1.1). The ERA5 site (112.1 ± 7.6 μg C L^{-1} d^{-1}) had the highest value among all studied water bodies.

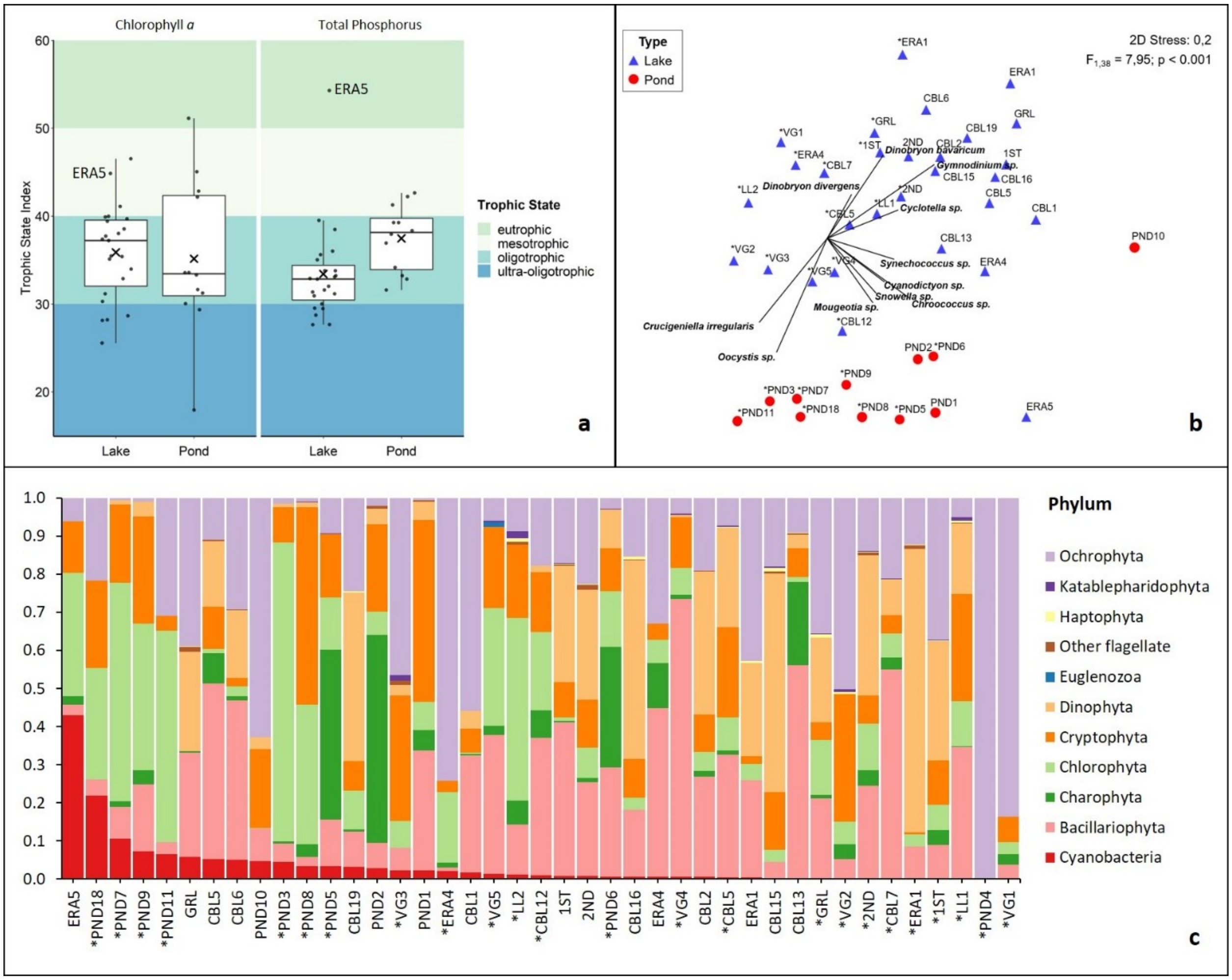

Figure 1. 2 a) TSI calculated for Chl a and TP for all lakes and ponds. Whiskers define the standard deviation. Means are represented by an X, medians by a line, dots are data. b) nMDS plot representing the community structure in each pond/lake. Shown vectors of taxa were selected based on their contribution as % to the difference between ponds and lakes, a few additional Cyanobacteria and Chlorophyta taxa were also included to illustrate the different communities observed in ERA5. c) Proportions of phytoplankton phylum by biovolume in waterbodies, ordered by presence of Cyanobacteria. All pond names start with PND. Lakes and ponds that were sampled in 2019 are marked with an asterisk (*).

The nMDS analysis based on the taxonomy of phytoplankton category biovolumes showed a highly significant difference between lakes and ponds ($F_{1,38} = 7.95$; $p < 0.001$) (Figure 1.2b). Although ERA5 is a lake because of its large surface area and connected to the main watershed drainage system, it grouped closer to the ponds (Figure 1.2b). Nevertheless, there was a clear difference in the phytoplankton composition, especially in the greater proportion of Cyanobacteria found in ERA5 as compared to the other lakes and ponds (Figure 1.2c). The biovolume of Cyanobacteria in ERA5 was greater than in any of the other 34 lakes and ponds and represented nearly 43% of the total phytoplankton biovolume in the lake (Table 1.1 and Figure 1.2c). Four cyanobacterial genera were identified in ERA5, the most abundant was *Chroococcus sp.* (24.2%), followed by *Cyanodictyon sp.* (13.2%), *Snowella sp.* (5.3%) and *Synechococcus sp.* (0.2%). The second most represented group was Chlorophyta with 32.3% of the total biovolume and four genera: *Pediastrum sp.* (11.2%), *Planctonema sp.* (11.2%), *Oocystis sp.* (5.4%) and *Crucigenia sp.* (4.5%). Two other sites, both ponds, had higher than 10% representation of Cyanobacteria (Figure 1.2c).

The satellite imagery suggested ERA5 has had an elevated trophic status for the last 30 years as evidenced by the constant light green color of the water through the years that contrasted with the

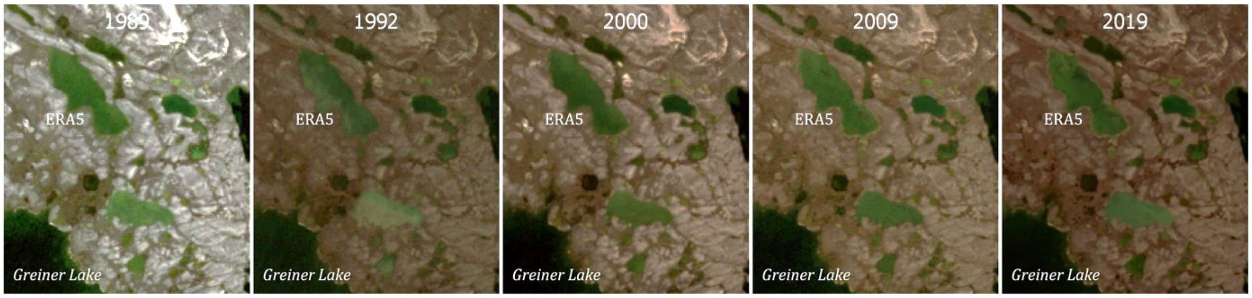

Figure 1. 3 Satellite images from 1989 to 2019 (Landsat 5TM 1989-2009 and 8 OLI 2019) of ERA5, including a section of Greiner Lake. All images are from August, courtesy of the U.S. Geological Survey (2020) and processed with Q-GIS 3.14.

darker blue color observed in Greiner Lake (Figure 1.3). Other green, likely eutrophic, lakes in the Greiner watershed occurred in the same area, close to ERA5.

1.5 Discussion

Lakes and ponds differed in their nutrient composition. A dilution effect in lakes appears to explain the lower nutrient concentration in larger water bodies as noted by Dranga et al. (2018), and is associated with larger surface area and depth. One lake, ERA5, however, was ranked as eutrophic according to both TP and Chl *a*, with a >40% prevalence of Cyanobacteria by phytoplankton biovolume. To our knowledge, this is the first time eutrophication from high TP and associated elevated Chl *a* concentrations has been reported in an Arctic lake without direct human impact. Interestingly, satellite imagery suggests other similarly high trophic state lakes are present in the same watershed (Figure 1.3).

Lakes in the Arctic are typically classified as ultraoligotrophic or oligotrophic according to their TP values (Lyons & Finlay, 2009). For Victoria Island, reported values from 95 lakes and ponds in previous studies have ranged from 0.01 $\mu g\ L^{-1}$ to 71 $\mu g\ L^{-1}$ (Dranga et al., 2018). P concentrations were high in six of these lakes and ponds located in the north of the island, but no other eutrophication indicators were reported. Hamilton et al. (2001) attributed the high values to the phosphorus-rich bedrock composition of the area associated with the volcanic formations at the northern end of the island (Williamson et al., 2013). The south of the island, near Cambridge Bay, sits over base-rich limestone till (McLennan et al., 2018) that tends to have lower P concentrations (Porder & Ramachandran, 2013). Hamilton et al. (2001) also indicated that although TP values were high, the type of phosphorus present was bound to particles and inaccessible to phytoplankton. This suggests the P found in ERA5 may come from the organic upper layer of the soil. Reported Chl *a* concentrations for 9 lakes in south Victoria Island, including Second Lake (2ND) analyzed in this study had a mean of 0.50 (±0.47) µg L^{-1} (Dranga et al., 2018). TN values in the same database had a mean of 366 (±170) µg L^{-1}. Almost 20 years later, our results in the same area indicate Chl *a* and TN values higher than either of these earlier studies (Table 1.1). This result is consistent with other studies that have indicated that Chl *a* values appear to be increasing and freshwater ecosystems have become more productive as a result of the rapid climate-driven changes affecting the Arctic (Hargan et al., 2020; Michelutti et al., 2005; Stuecker et al., 2018). Since Chl *a*, phytoplankton biomass and nutrients are positively correlated to mean July temperature (Dranga et al., 2018), small increases in temperature in the Arctic can have a major effect, especially in shallow water bodies that have been shown to respond rapidly to shifts in air temperatures (Rautio et al., 2011).

Other mechanisms contributing to the higher trophic status include permafrost thaw and increases in hydrological connectivity associated to higher temperatures. While no apparent changes in precipitation have taken place in the Cambridge Bay region for the last 50 years, temperatures have increased (Environment and Climate Change Canada, 2020), contributing to deeper soil thaw in summer and greening. Changes in catchment vegetation and the active layer modify the chemical composition of water that leaches out from soils rich in nutrients. Phosphorus and nitrogen supplements enter the lakes through water tracks and via passive transport (Harms et al., 2019), and stimulate primary production (Wauthy & Rautio, 2020). Further, ERA5 is located on the northern section of the Greiner watershed in an area that has the highest snow accumulation in the region (on average 85 cm versus the mean 35 cm for the region; A. Langlois lab, personal communication). It could be that the greater volume of snowmelt in spring moves associated nutrients from the watershed to ERA5, thereby contributing to eutrophication. The green colour in the nearby lakes (Figure 1.3; E. Imbeau, personal communication) further suggests that the high snow accumulation on the north shore of Greiner creates favorable conditions for phytoplankton growth.

Another explanation for high nutrient values in ERA5 and in some of the ponds, may be the presence of geese in the area (Jensen et al. 2019). Six species of geese nest on Victoria Island: Snow Goose (*Anser caerulescens*), Ross's Goose (*A. rossii*), Greater White-fronted Goose (*A. albifrons*), Brant (*Branta bernicla*), Cackling Goose (*B. hutchinsii*) and Canada Goose (*B. canadensis*) (Canadian Wildlife Service Waterfowl Committee, 2020; Hines et al., 2000; Kerbes et al., 2014; Lok & Vink, 2012). The White-fronted Goose and Brant are reported to have had large population increases in Canada since the 1970s (Canadian Wildlife Service Waterfowl Committee, 2020). Further, Snow Goose and Ross's Goose populations have increased across the Canadian Arctic to the point of being declared overabundant in 2014 (Canadian Wildlife Service Waterfowl Committee, 2020; Lefebvre et al., 2017). Geese foraging affects plant communities and their feces can change the chemical composition of soil and water, provoking eutrophication (Mariash et al., 2018b). Bird feces were noted around most lakes and ponds, with higher concentrations found in and around shallower water areas (P. Blackburn-Desbiens, unpublished data). Feces are a source of TP and TN and can trigger cyanobacterial blooms (Jensen et al., 2019; Mariash et al., 2019), but residence time, dictated by geomorphology would determine the likelihood of a persistent or annual recurring bloom. The area surrounding ERA5 is dominated by moderate slopes on the northern side of the lake and characterized by *Dryas integrifolia – Carex rupestris* plant associations that can range from 10 to 75% cover (Ponomarenko et al., 2019). The southernmost margin of the lake is dominated by two converging slopes and flat areas that are often flooded. *Carex* species are abundant and exposed to high levels of goose grazing and feces deposition, which increases nutrients in the soil and shallow waters (Ponomarenko et al., 2019) that are subsequently flushed to lakes, especially with high snowmelt.

The separation of lakes and ponds observed in the nMDS suggested an important difference in the phytoplanktonic composition between smaller, shallower water bodies and lakes (Figure 1.2b, Table S1.1). Phytoplankton in lakes were dominated by Dinophyta, Cryptophyta and Bacillariophyta, differentiating them from ponds where Chlorophyta were the most abundant taxa, as has also been shown elsewhere in the Arctic (Charvet et al., 2011; Sheath, 1986). ERA5, despite its large surface area and lake-like pelagic food web structure with fish at the top of the food chain, clustered close to the ponds. It is possible that the zooplankton community in this shallow lake was more typical of that of ponds, with large-bodied cladocerans applying a high grazing pressure on phytoplankton and shaping its community composition (Rautio & Vincent, 2006). More studies are required to accurately estimate the reasons for the phytoplankton community difference between ponds and lakes.

In subarctic ponds with Cyanobacteria, the richness and diversity of other phytoplankton species was generally low (Przytulska et al., 2017). As noted in Figure 1.2c, other phytoplankton groups were also less predominant in lake ERA5 compared to Cyanobacteria. Although the Cyanobacteria identified by microscopy did not include N_2-fixing species with heterocytes, increasing temperatures may promote their growth in high latitudes in the future (Woolway et al., 2020). For example, cyanobacterial algal blooms in subarctic freshwaters were reported when water temperatures exceeded 15°C during the summer (Gu & Alexander, 1993; Gu et al., 1996; Pick, 2016; Pokrovsky & Shirokova, 2013). However, cyanobacterial blooms have not been reported above the Arctic Circle, even in sewage-impacted Meretta Lake on Devon Island (Rigler, 1972, 1974), where temperatures have not reached 15°C to date.

The cyanobacteria found in ERA5, notably *Synechococcus*, are considered picocyanobacterial taxa and are frequently found in Arctic freshwaters (Lizotte, 2009; Vincent & Quesada, 2012). However, the high biovolume proportions may have been an underestimate since, due to their small size (0.8 – 3.0 µm), conventional light microscopy routinely misses these small cells. The relatively low total phytoplankton biovolume in ERA5 is explained by the small sized cells, making the high biovolume of cyanobacteria even more striking. Several small celled cyanobacterial groups, including the species of Chroococcales such as *Chroococcus* found in ERA5, are considered indicators of increasing P and high N concentrations (Andersson et al., 2015; Freeman et al., 2020) in addition to the green alga, *Pediastrum*, which was only found in ERA5, with a prevalence of 11.2% of phytoplankton biovolume (Table S1.1). *Pediastrum* has been associated with increased primary production driven by recent climate change in subarctic and high Arctic lakes (Rühland et al., 2013; Woelders et al., 2018).

Further, the high values of bacterial production in lake ERA5 indicate heterotrophic bacteria were actively decomposing organic matter (Hobbie & Laybourn-Parry, 2009) and likely contributing to the phytoplankton and, notably, the cyanobacterial biomass by converting unavailable organic P into dissolved available P. The high bacteria production was likely fueled by the high concentration of DOC (9.9 mg L^{-1}), which was the highest among the lakes studied. The *Carex* beds along the shore of ERA5 were a probable source of this DOC. Although the role of macrophytes in carbon cycling is unknown in the Arctic, it is known from boreal lakes that macrophyte leachates are an important source of energy for bacterial production (Findlay et al., 1986), which subsequently provides nutrients to the system. The role of macrophytes as a DOC source is also supported by the high DOC concentration in ponds that are frequently surrounded by macrophytes.

In summary, higher concentrations of nutrients, Chl *a*, DOC and bacterial production were more evident in ponds most likely due to their small size and isolated condition, which makes them highly responsive to nutrient and organic carbon inputs from the catchment as well as to increases in temperature. Although the relative contributions of the source inputs of the eutrophication process are still to be determined, our results also consistently point to a eutrophic lake ERA5 associated with high concentrations of nutrients and dissolved organic matter. Based on P concentrations, eutrophic conditions in lakes are already present in the Arctic in low numbers (Dranga et al., 2018). However, high P concentrations leading to high cyanobacterial dominance, without any apparent human impact, has not to our knowledge been previously reported for an Arctic lake. Interestingly, satellite imagery from ERA5 and nearby lakes and ponds suggests some sites have routinely had high Chl *a* concentrations for decades. This may also be related to the shallowness of the water bodies, since lakes and ponds with a light green colour found close to ERA5 (Figure 1.3) correspond to depths of less than 2 m reported by Ponomarenko et al. (2019). We argue that catchment and lake characteristics make some shallow lakes more susceptible/less resilient to eutrophication that is caused largely by different catchment inputs. Climate change stimulating nutrient enrichment in Arctic ecosystems suggests that a number of lakes will be predisposed to further eutrophication as conditions warm. Hence, the need for future research to establish whether, and how, increases in lake trophic states will affect resident phytoplanktonic communities and the rest of the food web in Arctic lakes and their downstream waters.

Arctic eutrophication could also affect water quality and may require closer monitoring of drinking water sources. In addition, eutrophication could become more widespread in a changing climate, as other components of the ecosystem, such as geese populations, move or expand with increases in plant cover as temperatures warm. Arctic coastal landscapes often feature vast low-lying areas dotted by lakes and ponds that are culturally connected to local Inuit. The proximity and connectivity of ERA5 and other potentially eutrophic lakes to Greiner Lake makes it advisable to monitor the waters of both ERA5 and Greiner given the importance of the latter as a drinking water source for the Ikaluktutiak Inuit. Our results further suggest that upstream information from watersheds is needed to provide useful context for understanding future changes in larger downstream lakes currently supporting local fisheries, such as in Greiner Lake that receives water directly from ERA5. While few Arctic limnological studies are conducted at the watershed scale, further investigation at such a scale, including studies on hydrological connectivity and paleolimnology, will provide an improved understanding of the processes driving Arctic lake trophic status, more accurate nutrient source information and dating of the onset of lake eutrophication processes.

1.6 Acknowledgements

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1.7 Supplementary material

Table S1. 1 Most common taxa (>5% biovolume present in at least 2 water bodies) in lakes and ponds from the Greiner Lake watershed and all sampled taxa in ERA5.

Phylum	Lakes	Ponds	ERA5
Bacillariophyta	*Asterionella formosa* *Cyclotella sp.* *Diatoma sp.* *Fragilaria crotonensis*	*Tabellaria fenestrata*	*Diatoma sp.* *Nitzschia sp.*
Charophyta	*Mougeotia sp.*	*Mougeotia sp.*	*Cosmarium sp.* *Elakatothrix gelatinosa*
Chlorophyta	*Nephrocytium sp.* *Oocystis sp.*	*Botryococcus sp.* *Crucigeniella irregularis* *Oocystis sp.*	*Crucigenia sp.* *Oocystis sp.* *Pediastrum sp.* *Planctonema sp.*
Cryptophyta	*Cryptomonas sp.* *Plagioselmis nanoplanctica*	*Cryptomonas sp.* *Plagioselmis nanoplanctica*	*Plagioselmis nanoplanctica*
Cyanobacteria	*Chroococcus sp.*	*Chroococcus sp.*	*Chroococcus sp.* *Cyanodictyon sp.* *Snowella sp.* *Synechococcus sp.*
Dinophyta	*Gymnodinium fuscum* *Gymnodinium sp.* *Peridinium sp.*	-	-
Ochrophyta	*Dinobryon bavaricum* *Dinobryon divergens* *Dinobryon sp.*	*Uroglena sp.*	*Chromulina sp.* *Dinobryon divergens* *Kephyrion/Pseudokephyrion sp.*

CHAPTER 2 LAKE METABOLISM

Dominance of net autotrophy in arid landscape low relief polar lakes, Nunavut, Canada

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2.1 Abstract

The Arctic is the fastest warming biome on the planet, and environmental changes are having striking effects on freshwater ecosystems that may impact the regional carbon cycle. The metabolic state of Arctic lakes is often considered net heterotrophic, due to an assumed supply of allochthonous organic matter that supports ecosystem respiration and carbon mineralization in excess of rates of primary production. However, lake metabolic patterns vary according to regional climatic characteristics, hydrological connectivity, organic matter sources and intrinsic lake properties, and the metabolism of most Arctic lakes is unknown. We sampled 35 waterbodies along a connectivity gradient from headwaters to downstream lakes, on southern Victoria Island, Nunavut, in an area characterized by low precipitation, organic-poor soils and high evaporation rates. We evaluated whether lakes were net autotrophic or heterotrophic during the open water period using an oxygen isotopic mass balance approach. Most of the waterbodies were autotrophic and sites of net organic matter production or close to metabolic equilibrium. Autotrophy was associated with higher benthic primary production, as compared to its pelagic counterpart, due to the high irradiance reaching the bottom and efficient internal carbon and nutrient cycling. Highly connected midstream and downstream lakes showed efficient organic matter cycling, as evidenced by the strong coupling between gross primary production (GPP) and ecosystem respiration, while decoupling was observed in some headwater lakes with significantly higher GPP. The shallow nature of lakes in the flat, arid region of southern Victoria Island supports net autotrophy in most lakes during the open water season. Ongoing climate changes that lengthen the ice-free irradiance period and increase rates of nutrient evapoconcentration may further promote net autotrophy, with uncertain long-term effects for lake functioning.

2.2 Introduction

The Arctic is warming at a much faster pace than the rest of the planet (Rantanen et al., 2022). Climate-driven changes in the functioning of inland waters are underway throughout the Arctic, as revealed through long-term monitoring and paleo-ecological records of both rivers and lakes (Smol et al., 2005; Tank et al., 2023; Walter Anthony et al., 2012). There is widespread concern that climate-induced shifts in Arctic ecosystem functioning could lead to enhanced carbon (C) processing and greenhouse gas (GHG) emissions, thereby causing positive climate feedback effects (Schuur et al., 2015). As northern inland waters are major sources of atmospheric GHGs (Lauerwald et al., 2023), and represent a disproportionately large percentage of the regional land surface (Downing et al., 2006), climate-driven shifts in aquatic C cycling have been forecast to have potentially large implications for the global climate system (Hastie et al., 2018). Yet the majority of data on Arctic and boreal (i.e., northern) lake C cycling is derived from concentrated areas (Bogard et al., 2019), and new studies are emerging that indicate a diverse range of lake C cycling patterns in less-studied Arctic (Brothers et al., 2021; Tank et al., 2009) and boreal (Bogard et al., 2019) regions, suggesting GHG emissions patterns in northern lakes may respond to climatic changes in divergent ways. For this reason, broader data collection is needed from other Arctic regions to gain a more representative understanding of lake sensitivities and responses to climatic change.

As biogeochemical hotspots on the landscape, lakes shape the fate of C through multiple pathways including processing, mineralization, and sequestration (Battin et al., 2009). In this context, understanding lake metabolism contributes to the knowledge of biological C turnover and consequently to the exchange of carbon dioxide (CO_2) with the overlying atmosphere (Duarte &

Prairie, 2005; Tranvik et al., 2009). Lake metabolic processes include rates of gross primary production (GPP) and ecosystem respiration (ER), and the balance of each is termed net ecosystem production (NEP). Rates of GPP capture primary production by photosynthetic organisms in pelagic, littoral, and benthic zones of the lake, and are dependent on resource availability (i.e., light and nutrients) and temperature (Padfield et al., 2017). In contrast, ER, the sum of respiration from all autotrophic and heterotrophic organisms, occurs across all habitats at rates that may vary depending on external organic matter delivery, species composition, and environmental conditions linked to time of day and season (Williams & del Giorgio, 2005). Currently, metabolic data on Arctic lakes are extremely limited in extent due to the difficulties in sampling in such remote regions.

Aquatic metabolism, and thus C cycling, are responsive to human activities including ongoing climatic and hydrological changes, eutrophication, and increased catchment disturbances that modify the transport of solutes into lakes (Oleksy et al., 2021; Solomon et al., 2015; Vadeboncoeur et al., 2003). Within this framework, the most commonly described controls of metabolic processes are nutrient and dissolved organic C (DOC) availability, light, and water temperature (Ask et al., 2009; Bergstrom & Karlsson, 2019; Staehr et al., 2010b). Most lake ecosystems are net heterotrophic and respire more organic matter than they produce (Bogard & Del Giorgio, 2016; del Giorgio & Peters, 1994; Mcdonald et al., 2013; Solomon et al., 2013). Additionally, hydrological connectivity to terrestrial environments delivers organic materials (Covino, 2017) that can stimulate heterotrophic bacterial respiration in excess of primary production (del Giorgio & Peters, 1994). Yet some productive lakes can be net autotrophic, with rates of GPP exceeding ER (Bogard et al., 2019; Pacheco et al., 2014). While nutrients are often determined by underlying bedrock, other external inputs such as animals' feces, and detritus from terrestrial vegetation

(Burpee & Saros, 2020) or atmospheric deposition (Holtgrieve et al., 2011) can also occur. Primary producers benefit from the increased input of allochthonous nutrients including nitrogen (N) and phosphorus (P) (Bogard et al., 2020; Hanson et al., 2003; Isles et al., 2021), which in northern oligotrophic lakes are largely derived from organic matter-bound sources. Under more extreme terrestrial loading, autotrophic growth can become limited by reduced light penetration linked to elevated colored organic matter content (Ask et al., 2012; Ask et al., 2009), though a recent study of many subarctic lakes indicates that widespread increases in DOC content could stimulate phytoplankton growth in most lakes (Isles et al., 2021). For Arctic lakes specifically, hydrological connectivity with a high terrestrial influence is typical in some regions with organic-rich catchments experiencing permafrost degradation (Wauthy et al., 2018). Here, extensive permafrost thaw (Biskaborn et al., 2019) has led to focused sampling that demonstrates large amounts of soil-derived organic matter inputs sustain high rates of C mineralization (e.g., Prėskienis et al., 2021; Walter Anthony et al., 2016). At the same time, Arctic warming is shortening ice cover duration and lengthening open water and production periods (Prowse et al., 2006), which has been shown to support lower rates of CO_2 emissions in some lakes (Brothers et al., 2021). While it is broadly assumed that net heterotrophy dominates in many high latitude lakes (e.g., Tranvik et al., 2009), other landscapes, including relatively cold, organic-poor areas without apparent permafrost thaw (such as the Canadian Arctic Archipelago) are underrepresented in the scientific literature, possibly leading to a biased view of lake C cycling in the Arctic (Metcalfe et al., 2018).

Here, we study metabolism in a set of clear-water lakes along a hydrological connectivity gradient in the Greiner Lake watershed, Victoria Island, Nunavut, in the Canadian Arctic. The overarching objective of this study was to define how hydrological connectivity and environmental characteristics shape lake metabolism in this understudied region. The watershed is in an arid, low elevation catchment (~1500 km^2 in area) where lakes are mostly small and shallow. The flat topography and the nature of the soil has also allowed the formation of abundant shallow, highly-irradiated lakes that may be connected to other lakes at the beginning of the summer, but disconnect as discharge subsides or surface water evaporates. In general, downstream lakes receive water from a large number of upstream lakes and are therefore more connected to the landscape. The connectivity gradient was determined through the lake's position in the catchment by the number of upstream lakes connected to it. We hypothesized that: a) shallow lakes with a low degree of hydrological connectivity would be rain-fed, receive little terrestrial nutrients or C, leading to low rates of GPP and ER and more balanced NEP. Conversely, b) deeper, highly connected lakes receive higher terrestrial C inputs, resulting in higher ER, while these allochthonous compounds have variable impacts on GPP (nutrient-driven stimulation, and light-restricted suppression of primary production). Finally, c) the rates of NEP and associated exchange of CO_2 with the atmosphere are directly linked to the availability of C, nutrients and light in these clear-watered Arctic lakes.

2.3 Methods

2.3.1 Study site

The Greiner Lake watershed is on Victoria Island, in the southern Canadian Arctic (69°10'35.72" N, 104°55'54.87" W) close to the Inuit Ikaluktutiak community (Cambridge Bay; Figure 2.1a-b). The watershed surface area is ~1500 km^2 and consists of approximately 6300 lakes, 84% having a surface area $\leq$ 5 ha and 96% an average depth $\leq$ 2 m (Figure 2.1c-d and S2.1). The area is characterized by mostly coarse glacial till and dolomitic/limestone bedrock that determines regional water pH (8.3 ± 0.2) (McLennan et al., 2018; Westover et al., 2009), and soils with low organic content (< 55%) on the top 10 cm (Seo et al., 2015). Annual mean air temperature (1981-2010) was -13.2 °C, mean annual rainfall was 72.1 mm, mean annual snowfall was 80.2 cm (Environment and Climate Change Canada, 2022; Levasseur et al., 2021), and the open water season lasts approximately 3 months.

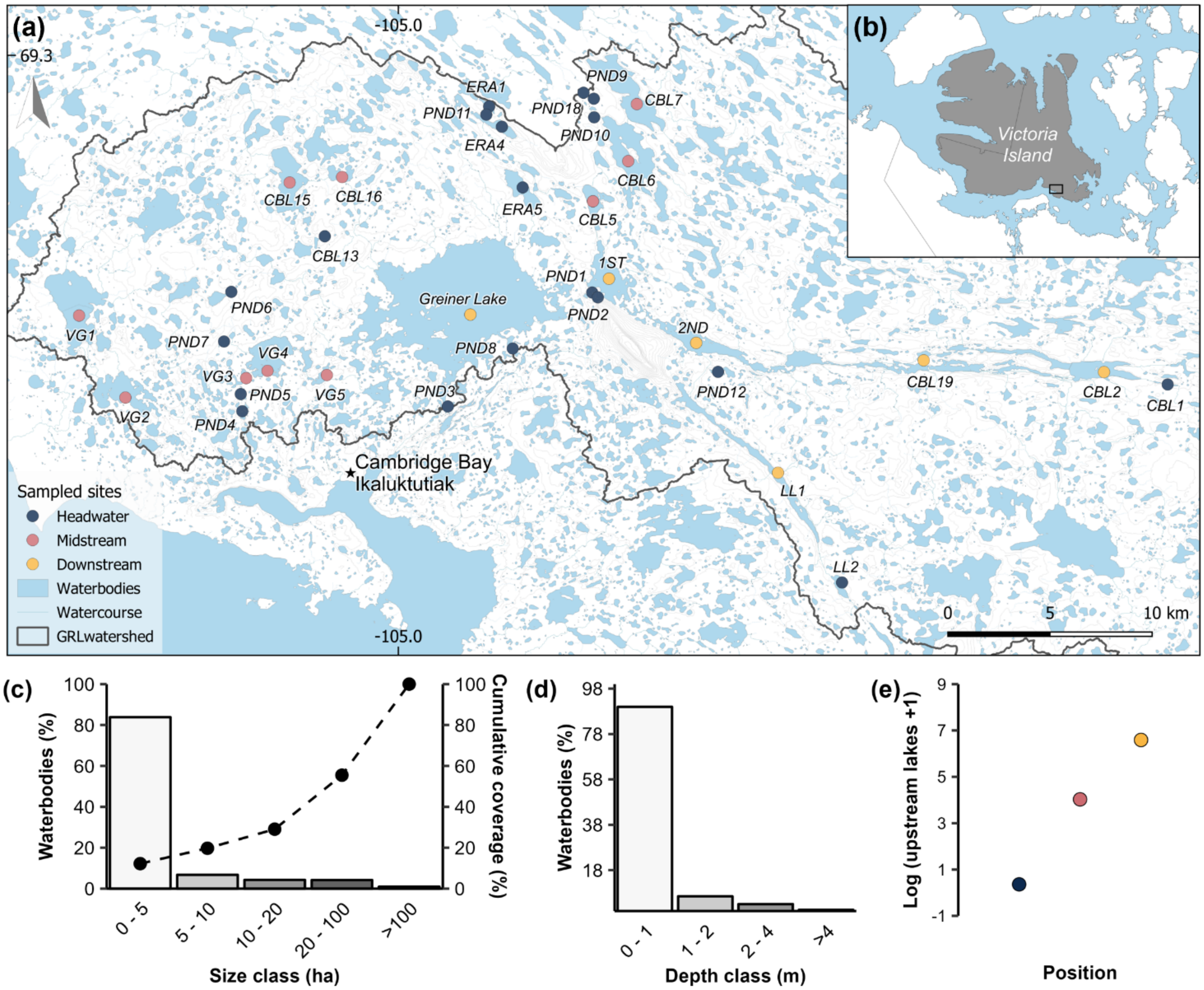


Figure 2. 1 a) Sampled lakes in the Greiner Lake watershed. b) Victoria Island, Nunavut, in relation to the Canadian Arctic Archipelago. c) Percentage of waterbodies grouped in five size categories (left y-axis; bars) and cumulative water coverage (right y-axis; dots). d) Percentage of waterbodies grouped in four depth classes. e) Mean number of upstream lakes for headwater (blue), midstream (pink) and downstream (yellow) lakes. Dots in e) represent average value with standard errors falling inside the dots. Note the log transformed y axis in e).

2.3.2 Connectivity and bathymetric measurements

In this study we define hydrological connectivity as the degree of contact of a given waterbody with its watershed. We thus use the number of upstream lakes to assign a connectivity category and use different metrics as proxies of connectivity to support the classification. Lake surface area, watershed area, and wetland coverage in individual watersheds for each sampled lake were calculated using QGIS 3.14 and Landsat 5TM and 8 OLI imagery (courtesy of the U.S. Geological Survey, 2020). Lakes smaller than 1 ha were measured using images from Google Earth Pro 7.3.4.8642. Watershed area was calculated using the *upslope area* tool of QGIS 3.14. Permanent streams in the watershed were determined from a flow accumulation matrix and enabled the calculation of the number of upstream lakes. For all sampled lakes with at least 200 ha of watershed, upstream connected lakes > 5 ha were enumerated. Lakes with smaller watersheds were disconnected from other lakes during sampling, therefore the number of upstream lakes was considered to be zero. Finally, the percentage of wetland cover was modelled based on the classification of Ponomarenko et al. (2019).

A combination of in situ depth measurements taken with a depth sounder (Hawkeye DT1H) or an echo sounder (Biosonics DT-X Extreme or Hummingbird; Rautio et al., 2022), were used to construct bathymetric maps. Interpolation was performed using the v.surf.rst tool from Grass GIS and the spline algorithm (Hofierka et al., 2009), with maps constructed using QGIS 3.14.

2.3.3 Sampling

A total of 35 waterbodies were sampled in the Greiner Lake watershed in August 2018 and 2019 (Figure 2.1a-b). Most lakes were sampled once, but 6 lakes (Greiner Lake, 1ST, 2ND, ERA1, ERA4 and CBL5) were sampled in both years. The sampled waterbodies were divided into three categories according to their degree of connectivity. These included: headwater lakes (N = 19) with 0 to <15 connected upstream lakes, midstream lakes (N = 11) with 15 to 100 upstream lake connections, and downstream lakes (N = 5) connected to more than 100 upstream lakes (Figure 2.1e).

For every lake, water temperature, conductivity, dissolved oxygen concentration (DO) and dissolved oxygen saturation (DO_{sat}) were measured with a multiparameter sonde (RBR Concerto, Ottawa, Canada). Photosynthetic active radiation (PAR) was measured in 19 lakes using a LI-COR light sensor logger (LI-1500). Water samples were taken at the deepest possible point or from the shore for lakes < 1 m deep. Samples for the measurement of $\delta^{18}O$ from dissolved oxygen ($\delta^{18}O$-O_2) were taken from surface water (0 to 30 cm depth) in gas tight exetainer vials loaded with $ZnCl_2$ as a preservative agent (Bogard et al., 2017). Additional samples from a subset of lakes were collected in April 2019 (Greiner Lake), and dissolved CO_2 samples were collected in May (Greiner Lake), July and August 2022 (9 lakes; See supplementary material). Water samples for all other analyses were collected using a 2L Limnos closing water sampler (Limnos, Poland) from several depths and combined as an integrated sample representing the water column that was thermally homogenous at all sites (Figure S2.2). Subsamples for DOC and dissolved inorganic carbon (DIC) were filtered with 0.45 μm polyethersulfone syringe filters into acid washed glass bottles. Unfiltered subsamples for total nitrogen (TN), and total phosphorus (TP) were taken in individual acid washed glass bottles. Samples for spectral characterization of dissolved organic matter (DOM) were filtered through a precombusted Whatman GF/F filter and stored in amber acid washed glass bottles. For $\delta^{18}O$ ($\delta^{18}O$-H_2O) and δ^2H (δ^2H-H_2O) isotopic data, subsamples of the integrated water column of all lakes, plus samples from headwater (N= 5), midstream (N= 7) and downstream (N= 4) streams, were collected and filtered through precombusted Whatman GF/F filters to airtight plastic vials. All samples were stored at 4°C until analyzed.

TP, TN, DIC, and DOC were analyzed by Environment and Climate Change Canada at the Burlington-National Laboratory for Environmental Testing following internal protocols (Environment Canada, 2019). $\delta^{18}O$ from dissolved oxygen ($\delta^{18}O$-O_2) was analyzed at the Veizer Stable Isotope Laboratory, University of Ottawa. Samples were equilibrated using a He matrix and were run against an oxygen reference gas and corrected to air following Barth et al. (2004). $\delta^{18}O$ and δ^2H from water were analyzed at UC Davis following the corresponding internal protocols, using CO_2-H_2O and H_2-H_2O equilibration methods and calibrated against VSMOW2, SLAP2 and GISP2 reference waters (International Atomic Energy Agency, 2017, 2021). Isotope values are reported in delta (δ) notation as in equation 2.1:

$$\delta^{18}O\text{-}O_2,\ \delta^{18}O\text{-}H_2O \text{ or } \delta^{2}H\text{-}H_2O = (R_{sample}/R_{standard})-1 \qquad (2.1)$$

where R_{sample} and $R_{standard}$ are the ratios of heavy to light isotopes ^2H:^1H or ^{18}O:^{16}O in the samples and standards of Vienna Standard Mean Ocean Water (VSMOW).

2.3.4 Spectral characterization of DOM

Chromophoric dissolved organic matter (CDOM) was characterized with spectrophotometric scans within 250 nm and 800 nm wavelengths using a quartz cuvette in a UV-visible Cary 100 (Agilent, Santa Clara, California). Fluorescent dissolved organic matter (FDOM) was measured with a Cary Eclipse spectrofluorometer (Agilent, Santa Clara, California) from 250 to 450 nm excitation wavebands (10 nm increments) and from 300 to 560 nm emission wavebands (2 nm increments) to obtain excitation-emission matrices (EEMs).

An absorption coefficient at 320 nm (a_{320}) was used as the DOM color indicator and calculated following Blough and Del Vecchio (2002). Specific ultraviolet absorbance ($SUVA_{254}$), as an indicator of aromatic DOM (Weishaar et al., 2003), was calculated using absorbance at 254 nm standardized to DOC concentration. Spectral slope for 279-299 nm (S_{289}) was calculated with a nonlinear regression fitting (Helms et al., 2008; Loiselle et al., 2009) as a proxy for autochthonous algal production (Roiha et al., 2015; Wauthy et al., 2018). Finally, a parallel factor analysis (PARAFAC) was performed to determine the main FDOM components in our samples. The model was run on MATLAB v R2013a (MathWorks, Natick, Massachusetts), following Murphy et al. (2013). The resulting components were compared with data available in OpenFluor (Murphy et al., 2014) and from the literature.

2.3.5 Irradiance calculations

The light attenuation coefficient (K_d) was calculated for all lakes where PAR was available. For lakes where PAR was not measured, K_d was calculated using the correlation between measured K_d and DOC as in Laurion et al. (1997). Finally, the percentage of irradiance at mean depth (Irradiance $\overline{z}$) was calculated for all lakes using equation 2.2:

$$Irradiance\ \bar{z} = 100 \times e^{-\bar{z} \times K_d} \qquad (2.2)$$

2.3.6 Production incubations using radioisotopes

Bacterial production (BP) was measured with incubations using the [^{3}H]-Leucine incorporation method (Kirchman, 2001). A sample of 1.2 mL of unfiltered water was spiked with [^{3}H]-Leucine (59 μCi ml^{-1}) and incubated at 10 °C ± 2 °C for 3 h. Incubations were stopped with 50% trichloroacetic acid (TCA). Control vials were identical except TCA was added before the incubation. Next, bacterial cells were concentrated by centrifugation at 12000 rpm, rinsed with 5% TCA and centrifugated again. The pellet was resuspended in a 1 mL scintillation cocktail and let sit for 24 h before radioactivity measurements were taken using a Perkin Elmer Tri-Carb 2910 scintillation counter. Leucine uptake was converted to C units using the standard conversion factor of 1.55 kg C $\mathrm{mol_{leu}}^{-1}$ multiplied by an isotopic dilution factor of 2 (Simon & Azam, 1989).

Primary production was measured in pelagic and littoral benthic compartments of five headwater lakes, three midstream and two downstream lakes with the incorporation of [^{14}C]-HCO_3, following Rae and Vincent (1998). Briefly, 20 mL of sieved lake water (<50 μm) for pelagic production, or 10 mm diameter benthic algal mats suspended in 20 mL of GF/F filtered lake water, were placed in duplicate acid washed glass vials. Samples were spiked with 50 μL (pelagic) or 25 μL (benthic) of [^{14}C]-HCO_3 (80 μCi ml^{-1}) and incubated *in situ* for 1 h immediately below the water surface. Incubation was carried out in a Rae box at 6 different light intensities (100%, 50%, 8%, 3%, 1%, 0% of incident solar radiation) that represent the downward irradiance in water. For total activity, 200 μl of the sample spiked with [^{14}C]-HCO_3 were removed and stored in tubes containing 200 μl of ethanolamine. After the incubation, the samples were kept in the dark until filtration through pre-combusted GF/F filters. Samples were acidified with 250 μl of HCl 0.5 N to remove unbound ^{14}C and stored in scintillation vials. Finally, 5 ml of scintillation cocktail were added to each sample and to the total activity vial and were left to sit for 24 h. Radioactivity was measured using a Perkin Elmer Tri-Carb 2910 scintillation counter. Maximum primary production (P_{max}) was assessed using the Platt equation as in Rae and Vincent (1998) using SigmaPlot 12.0.

2.3.7 Ecosystem production calculations

Following Bogard et al. (2017), GPP and ER (equations 2.3 and 2.4) were calculated using the oxygen isotope approach that considers the atom fractions of individual oxygen pools and fractionation factors (α) associated with gas exchange at the air-water interface ($\alpha_g = 0.9972$), gas solubility effects ($\alpha_s = 1.0007$), and photosynthetic DO production from H_2O ($\alpha_p = 1.000$):

$$GPP = \left(\frac{k_{O_2}}{Z_{mix}}\right) \times \frac{[DO \times (b-c) - DO_{sat} \times (a-c)]}{d-c} \tag{2.3}$$

$$ER = \left(\frac{k_{O_2}}{Z_{mix}}\right) \times \frac{[DO \times (b-d) - DO_{sat} \times (a-d)]}{d-c} \tag{2.4}$$

k_{O2} is the temperature-specific gas exchange coefficient (m d^{-1}) as in equation 2.5, and *Sc* is an O_2 temperature-specific Schmidt number (Wanninkhof, 1992):

$$k_{O2} = k_{600}\,(Sc/600)^{-1/2} \tag{2.5}$$

An empirical wind and lake area model was applied to obtain gas transfer velocity (k_{600}; equation 2.6) using wind speed at 10 m, in m s^{-1} (U_{10}) and lake area (LA) as in Vachon and Prairie (2013):

$$k_{600} = 2.51\,(\pm 0.99) + 1.48\,(\pm 0.34)\,U_{10} + 0.39\,(\pm 0.08)\,U_{10}\,log_{10}LA \tag{2.6}$$

Z_{mix} is the average lake depth (used here as the water column was fully mixed at sampling). DO and DO_{sat} are dissolved oxygen concentration and dissolved oxygen saturation, respectively. $a=AF_{atm} * \alpha_s * \alpha_g$, $b= AF_{DO} * \alpha_g$, $c= AF_{DO} * \alpha_c$ and $d= AF_{H2O} * \alpha_p$. Atomic fractions for dissolved oxygen (AF_{DO}), water (AF_{H2O}), and atmosphere (AF_{atm}) were calculated following Bogard et al. (2020), based on Hotchkiss and Hall (2014) as in equation 2.7, where *i* is the atomic fraction:

$$AF_i = R_{sample}/(1 + R_{sample}) \tag{2.7}$$

2.3.8 Water isotopes, sources of water and evaporation

The analysis of water isotopes was performed to determine the main sources of lake water, i.e., to estimate relative contributions of rain, soil water, snow, lake ice and water from upstream lakes through streams. Samples taken from lakes and streams were compared to isotopic data of different water sources sampled in summer 2018 available in the PANGAEA repository (Levasseur et al., 2020a, b). Additionally, deuterium excess (d-excess) was calculated for all lakes as a proxy for evaporation (Dansgaard, 1964) using equation 2.8:

$$d\text{-}excess = \delta^2\mathrm{H} - 8 \times \delta^{18}\mathrm{O} \tag{2.8}$$

where δ^2H and $\delta^{18}O$, respectively, are the hydrogen deuterium and oxygen isotope values of the samples expressed with respect to the VSMOW scale.

2.3.9 Data analyses

We used analysis of variance (ANOVA) followed by Tukey's post-hoc HSD test or the equivalent non-parametric Kruskal-Wallis test, when the ANOVA assumptions were violated, to assess differences in NEP, GPP, ER and all environmental variables across the three lake connectivity categories. Multiple correlation analyses were performed among all our variables to determine collinearity and select variables of interest. Coupling between GPP and ER was evaluated using a standardized major axis linear regression by applying the *smatr* library in R. Multiple linear regressions (MLR) to determine major drivers for GPP and ER were performed with *MuMin* library in R, using selected non-correlated variables. The variables tested included a combination of nutrients and DOM characteristics (TP, $SUVA_{254}$, S_{289} and FDOM components C1-C4), catchment characteristics potentially contributing to external inputs of nutrients and C such as number of upstream lakes, wetland coverage in the catchment and watershed area to lake area ratio (W:L), as well as irradiance $\bar{z}$ and BP that are known to contribute to metabolism. DOC and TN were omitted from the analyses due to their high negative correlation with d-excess ($r = -0.89$, $p < 0.001$ and $r = -0.84$, $p < 0.001$ respectively). DIC was omitted as it was negatively correlated with the number of upstream lakes ($r = -0.86$, $p < 0.001$). Outlier lake ERA5 was also omitted from the analysis. ER, W:L, TP, $SUVA_{254}$, C2 and BP were square root transformed, and the number of upstream lakes (+1) was log transformed prior to analyses. The best models were selected using the lowest Aikaike Information Criterion (AICc) corrected for small sample size (Anderson, 2008). Alternative models considered as plausible (i.e., within three AICc units of the best model) were also retained. The Akaike weights (w_i) of every retained model were used to calculate variable importance weights (Σw_i) for GPP and ER and to rank the relative importance of the variables considered by the MLR analysis (Symonds & Moussalli, 2010). All analyses were performed using R V4.1.2. (R Core Team, 2021).

2.4 Results

2.4.1 Hydrological connectivity and limnology

Headwater lakes were mostly shallow and smaller in size and volume than midstream or downstream lakes (Figure 2.1c-d and Table 2.1). However, some maximum depths in mid and downstream lakes exceeded 20 m. Mean temperature at sampling for all lakes was 10.2 ± 1.5 °C. All water columns were mixed as evidenced by temperature and oxygen profiles (Figure S2.2). The W:L ratio for headwater lakes was lower compared to highly connected midstream and downstream lakes (Figure 2.2a, Table 2.1). The percentage of wetland coverage for all catchments was below 35%, but headwater lakes had significantly lower percent coverage compared to the other categories (Figure 2.2b). The percentage of irradiance reaching the bottom at the mean depth of the lakes was significantly higher in headwater compared to downstream lakes, while midstream

Table 2. 1 Range of values in every lake category for connectivity variables, physicochemical variables, and colorimetric and fluorometric properties.

Variable	**Units**	**Headwater (n=21)**	**Midstream (n=12)**	**Downstream (n=8)**
Maximum depth	(m)	0.4 - 10.8	2 - 32	6.1 - 23
Lake area	(ha)	0.07 - 141.32	19.57 - 610.83	92.34 - 3873.72
Watershed area	(ha)	2.49E+00 - 2.07E+03	4.23E+03 - 1.39E+04	7.36E+04 - 1.62E+05
Lake volume	(m^3)	3.45E+02 - 1.45E+06	2.71E+05 - 2.09E+07	2.14E+06 - 9.88E+07
Water temperature	(°C)	5.6 - 13.9	7.9 - 10.9	9.3 - 12.3
W:L	-	2.6 - 161.4	9.7 - 571	41.8 - 895.6
Wetland coverage	(%)	7.8 - 31	23.1 - 31.4	29.8 - 33.79
Irradiance $\bar{z}$	(%)	16.4 - 66.7	2.2 - 78.8	15 - 36.6
DIC	(mg L^{-1})	24.2 - 39.6	16.2 - 22.5	13.3 - 16.8
DOC	(mg L^{-1})	3.8 - 19.7	3.6 - 6.1	3.7 - 6.1
TP	(µg L^{-1})	5.1 - 32.3	5 - 11.6	5.4 - 10.6
TN	(µg L^{-1})	322 - 1440	281 - 558	273 - 832
N:P	-	13 - 67	15 - 37	18 - 45
BP	(mg C m^{-3} d^{-1})	3.1 - 124.4	18.6 - 43	8.8 - 47.8
SUVA$_{254}$	(L mg C^{-1} m^{-1})	0.91 - 4.55	0.53 - 2.09	1.34 - 2.47
a_{320}	(m^{-1})	3.12 - 25.98	3.21 - 6.63	5.47 - 8.06
S$_{289}$	(nm^{-1})	0.023 - 0.031	0.023 - 0.029	0.021 - 0.025
C1	(%)	3.4 - 70.7	0 - 66.9	0 - 78.3
C2	(%)	0 - 63.7	0 - 72.9	0 - 62.6
C3	(%)	6.5 - 85.6	11.1 - 71	14.1 - 70.1
C4	(%)	3.4 - 27.2	3.5 - 26.4	5.9 - 18.5

Higher C and nutrient concentrations were found in headwater lakes, compared to downstream lakes (Figure 2.2d-g, Table 2.1), with one eutrophic lake occurring as an outlier (ERA5 with TP 32.3 μg L^{-1}). N:P molar ratios were highest in headwater lakes and reduced along the gradient with lower values in midstream and downstream lakes (Figure 2.2h). The N:P molar ratio calculated from TN and TP concentrations in headwater lakes showed P limitation with mean values above 30 (Downing & Mccauley, 1992) and N limitation in midstream and downstream lakes where mean values were below 25 (Elser et al., 2009). There were significantly higher values in headwater lakes compared to both midstream and downstream lakes for DIC, DOC, TN and N:P ratio (ANOVA, $p < 0.001$), but midstream lakes did not differ significantly from downstream lakes. BP was similar in most lakes, with no significant differences among categories. However, the highest values were registered in headwater lakes (Figure 2.2i, Table 2.1). Correlation analysis indicated a strong negative correlation among connectivity variables, i.e., watershed area, lake volume and lake surface area, with DOC and DIC (Spearman's rho < -0.75, p-value < 0.01). DOC in turn was strongly correlated to TN (Spearman's rho -0.96, p-value < 0.01).

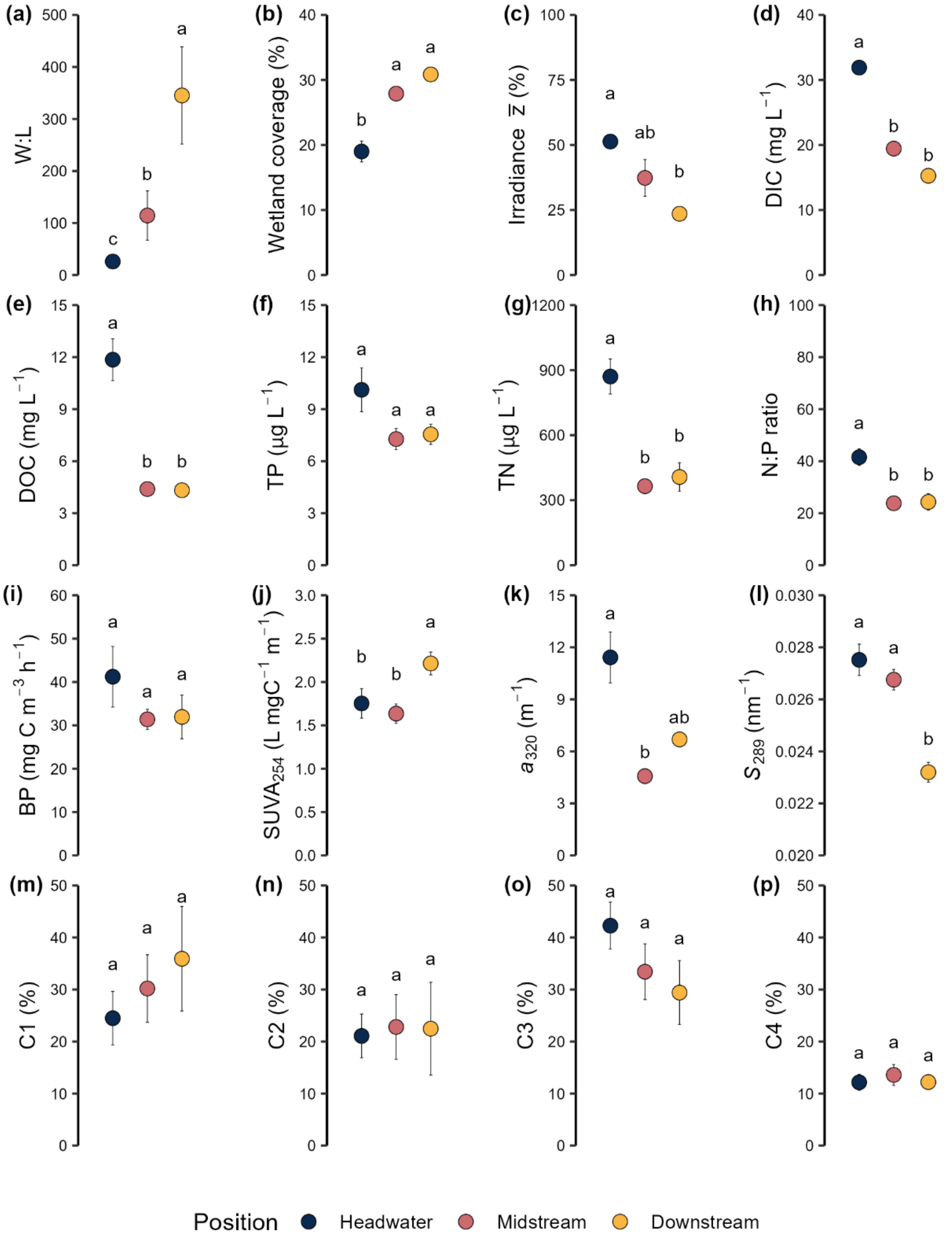


Figure 2. 2 Mean value and standard errors of physical, chemical, and biological variables of studied lakes, classified by their position in the watershed. a) watershed to lake ratio (W:L), b) percentage of wetland coverage in the watershed, c) percentage of irradiance at mean depth, d) dissolved inorganic carbon, e) dissolved organic carbon, f) total phosphorus, g) total nitrogen, h) N:P molar ratio, i) bacterial production, j) specific UV absorbance at 254 nm, k) absorption coefficient at 320 nm, l) spectral slope for 279-299 nm, m) to p) percentage of fluorescent organic matter components obtained with PARAFAC. Letters on each plot indicate differences among groups based on ANOVA (α=0.05) and post-hoc Tukey's test, colors indicate position in the watershed.

2.4.2 Characteristics of DOM

Colorimetric characterization of the water in all the lakes showed low aromatic compounds content as represented by $SUVA_{254}$, with no significant differences between headwater and midstream lakes, but significantly higher values between downstream lakes and the two other categories (Kruskal-Wallis, $p < 0.01$; Figure 2.2j). CDOM content (expressed as a_{320}) was significantly greater in headwater (Table 2.1) relative to midstream lakes (ANOVA, $p < 0.001$), but downstream lakes were not significantly different from either category (Figure 2.2k). The spectral slope (S_{289}) decreased from headwater to downstream lakes (Figure 2.2l, Table 2.1), with a significantly lower values (ANOVA, $p < 0.001$) evident for downstream lakes compared to headwater or midstream lakes.

PARAFAC produced four FDOM components (C1 to C4; Figure 2.2m-p, Table 2.1, Table S2.1 and S2.2). C1 and C2 are humic-like components mostly associated with terrestrial organic matter (e.g., Amaral et al., 2016; Kothawala et al., 2014). C3 is a protein-like component with tyrosine properties (e.g., D'Andrilli et al., 2017) and C4 resembles protein-like autochthonous microbial material with tryptophan properties (e.g., Stedmon & Markager, 2005). On average, all lakes had a higher proportion of protein-like components (C3 and C4) indicative of important sources of C production within lakes, with lower proportions of humic-like terrestrial components (C1 and C2).

2.4.3 Lake metabolism

GPP and ER values were obtained for 34 out of 35 lakes sampled in August 2018 and 2019, with 6 additional values for lakes sampled in both years (Figure 2.3a-b), 7 aberrant values such as negative ER values were removed, giving a total of 33 observations: 16 observations for headwater lakes, 9 for midstream lakes and 8 for downstream lakes. GPP ranged from 0.4 to 4.9 g O m^{-3} d^{-1} in headwater lakes, 0.1 to 2.6 g O m^{-3} d^{-1} in midstream lakes and 0.1 to 1.5 g O m^{-3} d^{-1} in downstream lakes, with significant differences existing only between headwater and downstream lakes (ANOVA, $p < 0.05$). Rates of ER ranged from 0.05 to 5.1 g O m^{-3} d^{-1} in headwater lakes, 0.1 to 2.9 g O m^{-3} d^{-1} in midstream lakes, and 0.01 to 1.4 g O m^{-3} d^{-1} in downstream lakes, with no significant differences existing among the lake types.

Most lakes were net autotrophic, i.e., 12 of 16 headwater, 6 of 9 midstream, and 6 of 8 downstream lakes had NEP > 0 (Figure 2.3c). The largest range of NEP was found in headwater lakes (-0.61 to 3.10 g O m^{-3} d^{-1}), with the highest values occurring in small, headwater lakes PND7, PND9, PND12, PND3 and the eutrophic headwater lake ERA5. NEP in midstream and downstream lakes showed less variation, ranging from -0.27 to 0.6 in midstream and -0.08 to 0.1 g O m^{-3} d^{-1} in downstream lakes. Although no significant differences were found among the lake groups, midstream and downstream lakes had NEP values closest to zero. Some lakes sampled in 2018 and 2019 showed different NEP between sampling years (ERA1, CBL5, 1ST, 2ND, Greiner Lake), appearing autotrophic one year and heterotrophic the next, or vice versa, but with little separation from equilibrium in either year. ERA1 was the only lake sampled in both years that showed a larger difference in metabolic state, going from net heterotrophic (-0.26 g O m^{-3} d^{-1}) in 2018 to net autotrophic (0.62 g O m^{-3} d^{-1}) in 2019. Seasonal differences in CO_2 concentration were further confirmed with results for a subset of lakes sampled in 2022. The tenfold differences in Greiner Lake CO_2 concentration in winter (mean ± SD, 280 ± 68 μM) compared to summer (July: 21.4 ± 4.1 μM, August: 26.1 ± 4.7 μM) highlighted the importance of CO_2 accumulation under ice (Figure S2.3a). Other lakes sampled in July were under-saturated in CO_2 respect to the atmosphere, although values increased above saturation in August for PND1 and PND2 (Figure S2.3b).

However, most lakes sampled in August were at atmospheric equilibrium or under-saturated in CO_2 (Figure S3b). For Greiner Lake, GPP:ER was > 1 during the ice-free period, indicating autotrophic conditions during summer 2018 and 2019, but becoming net heterotrophic in winter (GPP:ER < 0.3, Figure S4).

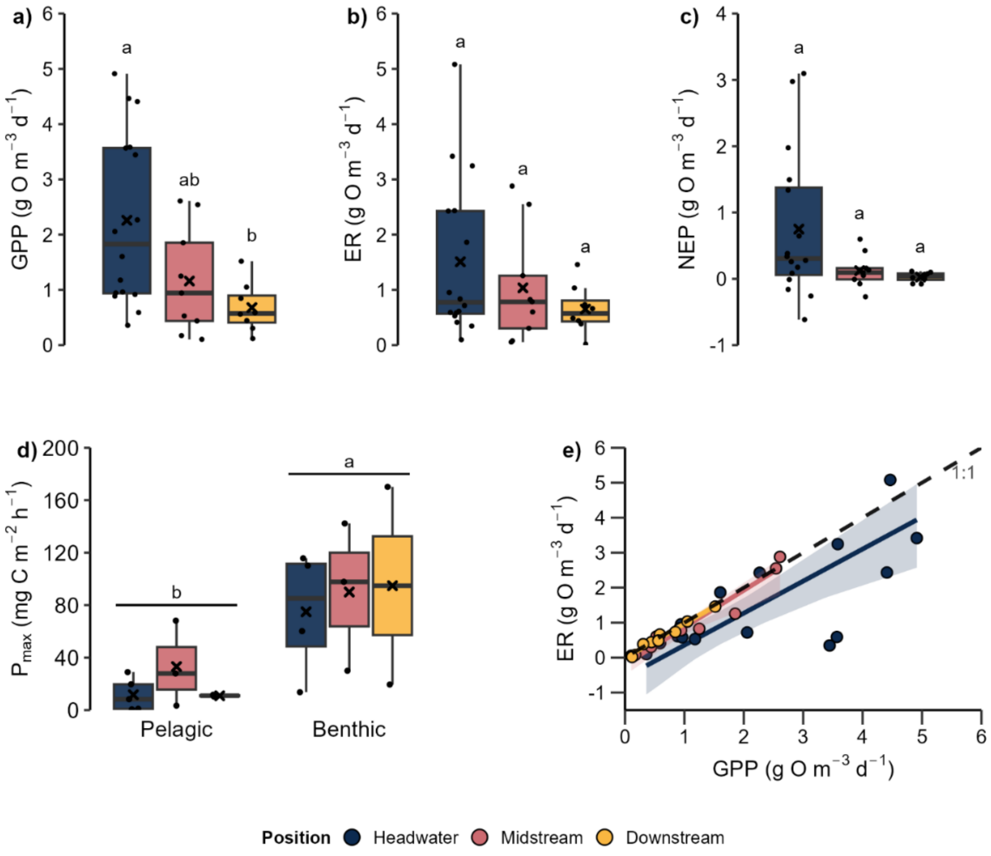


Figure 2. 3 Box plots of a) Gross primary production (GPP), b) Ecosystem respiration (ER), c) Net ecosystem production (NEP). d) Average maximum primary production in a subset of headwater, midstream and downstream lakes in the pelagic (Pel) and benthic (Ben) compartments, measured through incorporation of $[^{14}C]$-HCO_3. e) Major axis linear regression of GPP and ER in all sampled lakes with 95% confidence interval in gray. Colors indicate the position of the lakes in the watershed, headwater (blue), midstream (pink), downstream (yellow). X symbol in a), b), c) and d) represents means, dashed line in e) is the 1:1 coupling line. Volumetric production in pelagic samples in d) were converted to area by multiplying the values by lake average depth. Letters on each plot indicate differences among groups based on ANOVA (α =0.05) and post-hoc s Tukey's test, colors indicate position in the watershed.

Primary production was dominated by benthic production in a subset of lakes (Figure 2.3d) where mean benthic P_{max} was 4.7-fold higher (mean ± SD, 84.4 ± 56.2 mg C m^{-2} m^{-1}) than pelagic P_{max}

(18.0 ± 20.4 mg C m^{-2} m^{-1}; ANOVA, $p<0.01$). Only one high pelagic P_{max} value was found in midstream lake CBL5 (68.2 mg C m^{-2} m^{-1}). Benthic P_{max} results showed great variability, but no pattern among lake groups was observed.

Rates of ER were significantly correlated with GPP in midstream ($p < 0.001$, $R^2 = 0.94$) and downstream lakes ($p < 0.001$, $R^2 = 0.97$; Figure 2.3e). In headwater lakes the coupling between ER and GPP was significant but weaker than in the other groups ($p < 0.05$, $R^2 = 0.52$). None of the regression slopes differed significantly from 1 ($p > 0.5$). Larger intercept values for midstream and downstream lakes indicated elevated baseline rates of ER compared to headwater lakes.

2.4.4 Evaporation and sources of water

The water isotope results showed that evaporation occurred in all lakes, as evidenced by the enrichment of $\delta^{18}O$ relative to source waters (Figure 2.4a-b). A larger difference between headwater lakes and the local meteoric water line (LMWL) indicated higher evaporation rates for smaller and less connected waterbodies. High evaporation rates were confirmed by d-excess values that were significantly lower for headwater (mean ± SD, -7.2 ± 3.9 ‰) compared to midstream (-2.6 ± 18 ‰) and downstream (-1.3 ± 1.8 ‰) lakes (ANOVA, $p < 0.001$; Figure 2.4c). Further, water isotopes indicated that the main sources of lake water were rainfall, runoff from soil, and seasonally melted lake ice. More depleted isotopic values closer to the LMWL were found in midstream and downstream lakes, reaching the lowest value in Freshwater Creek which is the river outlet for the entire watershed (e.g. down-stream value in Figure 2.4a-b).

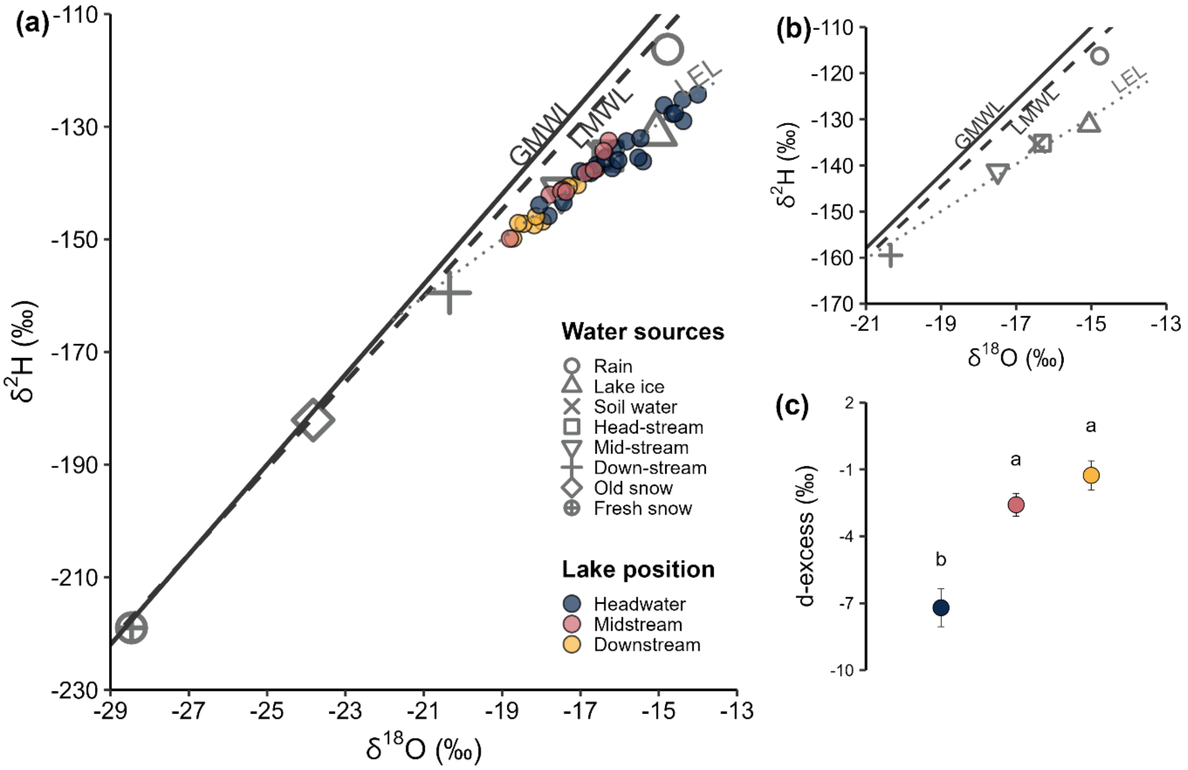


Figure 2. 4 a) $\delta^{18}O$ and $\delta^{2}H$ composition of lakes from the Greiner Lake watershed, sampled in 2018 and 2019 classified by their position in the watershed as headwater (blue), midstream (pink), and downstream (yellow). Reference sources of water were obtained from (Levasseur et al., 2021; Levasseur et al., 2020a, b) for the same study site in 2018. The grey continuous line illustrates the Global Meteoric Water Line (GMWL; $\delta^{2}H = 8*\delta^{18}O + 10$ ‰), the dashed line illustrates the Local Meteoric Water Line (LMWL; $\delta^{2}H = 7.66*\delta^{18}O + 0.83$ ‰) and the dotted line represents the Local Evaporation Line (LEL) obtained from the regression line of the sampled lakes. b) Water sources alone. c) d-excess for the headwater, midstream and downstream lakes. Letters indicate differences among groups based on ANOVA ($\alpha = 0.05$) and post-hoc Tukey's test.

2.4.5 Drivers of lake metabolism

The strongest multiple linear models explaining among-lake variation in GPP and ER had low Akaike model weights, 0.19 and 0.13 respectively, and for both GPP and ER there were numerous alternative plausible models (see Table S2.3 for a summary of results). Using the variables contained within the subset of models defining the 95% confidence interval, variable importance weights were used to select a subset of variables with high predictive strength ($\Sigma w_i > 0.75$) including TP, %C4, and Irradiance $\bar{z}$ (Table 2.2), which combined to explain 71% of the observed variation in GPP (Table S2.3). Irradiance $\overline{z}$ and TP had higher partial R^2 values, 0.47 and 0.44 respectively, while the partial R^2 for %C4 equaled 0.24. The most important predictors of ER were TP, Irradiance $\overline{z}$ and BP (Table 2.2), which combined with wetland coverage and d-excess in the best model to explain 53% of the observed variation (Table S2.3). TP and Irradiance $\overline{z}$ had the highest partial R^2 values, 0.12 and 0.29, respectively, while BP and d-excess (negatively correlated with ER) and wetland coverage (positively correlated) had partial R^2 values of 0.10, 0.05 and 0.04, respectively.

Table 2. 2 The overall importance weights (Σw_i) for each environmental predictor variable used in the GPP and ER models (described in Table S2.3). The most important variables for explaining variation in the dependent variable are bolded.

Variables	***Σw_i GPP***	***Σw_i ER***
TP	**+ 1.00**	**+ 1.00**
% C4	**+ 1.00**	+ 0.24
% Irradiance $\bar{z}$	**+ 1.00**	**+ 1.00**
S_{289}	+ 0.38	0.00
BP	- 0.18	**- 0.95**
% C1	+ 0.11	+ 0.20
d-excess	- 0.11	- 0.18
% C3	- 0.09	- 0.05
$SUVA_{245}$	- 0.06	+ 0.06
W:L	- 0.06	0.00
Upstream lakes	- 0.05	+ 0.05
% C2	0.00	- 0.11
% Wetland coverage	0.00	+ 0.39

2.5 Discussion

Our results show a dominance of net autotrophy in Arctic lakes of the Greiner Lake watershed during ice free periods, with the highest NEP values found in headwater lakes. However, most NEP values remained close to zero indicating a general trend towards equilibrium between ER and

GPP, especially in highly connected downstream lakes. Our results are consistent with studies from similar northern arid regions and indicate that autotrophic metabolism, with limited processing of terrestrial organic matter, and aquatic CO_2 content during the summer seasons are not uncommon for many Arctic lakes (Andersson & Brunberg, 2006; Bogard et al., 2019; Brothers et al., 2021; Tank et al., 2009).

2.5.1 Connectivity, limnology and lake metabolism

The biogeochemical differences among headwater, midstream and downstream lakes are likely associated with the position of the lakes along the headwater-downstream connectivity gradient, and differences in lake size and depth. Headwater lakes receive water primarily from precipitation, either directly or as lateral inputs from the catchment. Headwater lakes thus likely receive higher DIC directly from carbonate weathering of underlying limestones and CO_2 respired in the surrounding active layer. Furthermore, small, shallow lakes contain a lower volume of water and are prone to higher evapotranspiration rates that increase the concentration of solutes (Abnizova et al., 2014). Accordingly, headwater lakes showed significantly higher concentrations of DIC, DOC and TN that were likely consumed by autotrophic production, while larger downstream lakes had a lower solute to volume ratio, due to dilution in larger lake volume. Additionally, headwater lakes and surrounding wetland areas are ideal habitat for geese, and generally have abundant goose droppings (Cadieux et al., 2005) that are an important source of nutrients, especially N, for small waterbodies (Jensen et al., 2019; Mariash et al., 2019). The dominance of concurrent CO_2 supersaturation with autotrophic metabolism, plus terrestrial DIC delivery in headwater sites demonstrates that the headwater lakes surveyed here act more as chimneys that facilitate the emission of terrestrial CO_2 to the atmosphere. Thus, the insights gained from pairing metabolic and C cycling data provide important information about terrestrial-aquatic connectivity and lake

C sources and can help to avoid double counting the CO_2 generated in terrestrial habitats but transferred to aquatic networks prior to atmospheric emission.

The most extreme cases of net autotrophy existed in headwater lakes, linked to the high concentration of nutrients and the availability of carbonates. Lake metabolism is strongly influenced by benthic primary production in shallow oligotrophic clearwater lakes (Vadeboncoeur et al., 2008), where greater contact between the water column and the benthos exists. Light availability at the lake bottom enhanced benthic primary production, especially in small headwater lakes (mean depth < 1 m) where P_{max} in benthic zones exceeded that in pelagic waters. In these shallow headwater lakes, the higher percentage of light reaching the bottom supported the development of thick and photosynthetically active benthic microbial mats that dominated lake metabolic contributions, as has been noted for shallow lakes elsewhere (e.g., Quesada et al., 2009). However, in the larger, deeper, downstream lakes, benthic production in the littoral area played a smaller role in ecosystem production due to the larger water volume relative to the area of the photosynthetically active benthic region. This, plus lower nutrient, organic and inorganic C concentrations, resulted in lower rates of GPP and a more balanced metabolism in mid- and downstream lakes. Thus, our results highlight how the relative contribution of benthic versus pelagic production to ecosystem GPP can shift along the connectivity gradient. Our systematic survey of lake metabolism throughout the lake network shows that the metabolic balance and rates of NEP shift predictably with changes in lake morphometry (Klaus et al., 2022), that enabled a larger benthic productive surface in shallow, flat bottomed headwater lakes. To assess the role of changing lake depth in shaping metabolic patterns along the connectivity gradient, a subset of lakes of similar depths were analyzed (Figure S2.5). When compared to the whole data set, we observed that GPP and ER values were lower in the subset, showing the leverage of shallower lakes on the metabolic results. However, NEP trends in the subset remained consistent with the trends in the whole data set, as did most physicochemical variables, thus supporting the notion that changes in connectivity were more important than depth in structuring metabolic patterns, particularly NEP.

Rates of baseline respiration (as suggested by the intercept of the ER vs. GPP linear model) decreased from headwater to mid- and downstream lakes, indicating that possible terrestrial inputs, or organic matter fixed in previous seasons that had persisted into the summer, supported the greatest heterotrophic metabolic activity in the headwater systems, but that overall heterotrophy was quite limited. A similarly small intercept value for ER vs. GPP relationships has also been reported for shallow boreal lakes in Alaska (Bogard et al., 2019). Further evidence of low external input to downstream lakes consisted of the decreasing TN and C concentrations in the connectivity gradient through internal lake metabolic processes and nutrient retention (Wu et al., 2022) as water traveled downstream. Both may become locked up in headwater lakes as summer progresses and downstream connectivity is lost (White et al., 2014), as noted for headwaters in our study where d-excess values were low compared to the other lakes. A strong coupling of GPP and ER found in oligotrophic and dystrophic lakes elsewhere (e.g., Martinsen et al., 2017) has been attributed to the nature of the respirable organic matter coming mostly from autochthonous production instead of additional allochthonous organic matter that would increase rates of ER independently and in excess of GPP (Solomon et al., 2013).

2.5.2 Dominance of internal sources of DOM

We found several indicators of the predominance of internal organic matter sources in the studied lakes. First, the low absorbance coefficient of water at 320 nm indicated low levels of colored organic matter, suggesting that the lakes in the Greiner watershed are weakly affected by terrigenous/permafrost thaw material, and differ greatly from thermokarst lakes found in organic-rich permafrost (e.g., Rantala et al., 2016). We confirmed the difference using a_{320} and DOC linear regressions and by comparing lakes in this study to a subset of data from organic-rich thermokarst lakes and rocky-tundra lakes (Wauthy et al., 2018; Figure 2.5). Results showed our study slopes are low (slope = 0.9) and similar to lakes within rocky or tundra landscapes (slope = 1.1) when compared to thermokarst lakes (slope = 5.8), indicating little effective input of colored allochthonous organic matter in our lakes (ANOVA, $p < 0.001$). We also found that absorption values in the Greiner Lake watershed were similar to those from other studies of high latitude lakes (Roiha et al., 2016; Saros et al., 2016). We attribute the low external organic input to our study lakes to the organic-poor active layer covering Southern Victoria Island (McLennan et al., 2018).

The isotopic composition of the water (-149.9 to -124.3 $\delta^2H\text{-}H_2O$ and -18.8 to -14.0 $\delta^{18}O\text{-}H_2O$) further confirmed that, during the open water season, water in lakes of the Greiner watershed comes mostly from precipitation and lateral overland runoff from soil and water tracks (Levasseur et al., 2021). Rainfall in the region during summer is low (~72.1 mm y^{-1}) and all studied lakes, but especially small headwater lakes, are affected by evaporation as was evidenced by the enrichment in $\delta^{18}O$ and δ^2H, and the deviation of values from the global and local meteoric water lines and d-excess, as has been noted in other arid Arctic regions (Johnston et al., 2020). Although seasonal variability in DOM inputs could occur, results from comparable sites in the arid region of the Yukon Flats Basin in Alaska (Johnston et al., 2020) exhibited no significant seasonal changes. Thus, low precipitation regimes decrease the probability of soil-derived DOM inputs and lead to weaker terrestrial connectivity between the catchment and lakes (Bogard et al., 2019; Osburn et al., 2019; Osburn et al., 2017) as compared to wetter Arctic regions (Kellerman et al., 2020).

The properties and composition of DOM also point to the importance of internal organic matter production. The DOM in our lakes had low aromaticity ($SUVA_{254}$), and higher values of S_{289} that were similar to those reported by Wauthy et al. (2018) for tundra and rocky lakes, but unlike values for lakes within organic-rich permafrost. All $SUVA_{254}$ values in this study were lower than those for rocky or tundra lakes reported in Wauthy et al. (2018), showing a general low aromatic content. Nevertheless, when the lakes in this study were compared among each other, significantly higher $SUVA_{254}$ values suggesting higher terrestrial input in downstream lakes were observed, which is consistent with our hypothesis that more strongly connected downstream lakes may have higher allochthonous C inputs.

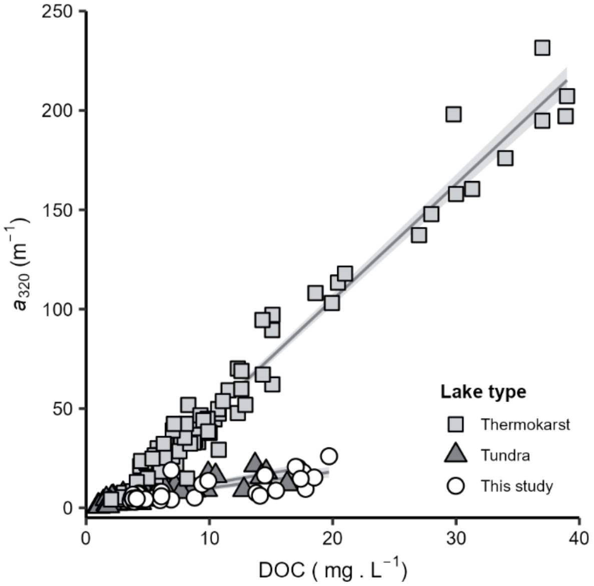


Figure 2. 5 Linear regressions of dissolved organic matter absorbance at 320 nm vs. DOC, comparing lakes in this study (circles), and a subset of lakes taken from Wauthy, et al. (2018), who report data from lakes in landscapes dominated by rocky tundra substrates (triangles) and thermokarst lakes (squares).

FDOM composition showed a higher proportion of C3, a protein like substance, in headwater lakes with the highest GPP and NEP values (PND12, PND3, PND9 and ERA5). An increasing proportional content of humic like (C1) and decreasing proportional content of protein like (C3)

FDOM has been linked to the increasing degree of hydrologic connectivity of lakes in other dry boreal and Arctic regions (Johnston et al., 2020; Tank et al., 2011). Unlike in those studies, no significant differences were found between the three groups of lakes for any of the components in this study. The difference may be due to the shorter environmental gradients in our watershed, compared to past studies conducted over broader spatial and hydroclimatic gradients. Both protein-like components found in this study (C3 and C4) are common indicators of internal microbial metabolism (Andersson et al., 2018; Kothawala et al., 2012) and freshly internally produced organic matter (D'Andrilli & McConnell, 2021). Similar protein-like compounds related to the dominance of bacterial metabolism in winter were also abundant in the studied lakes (Imbeau et al., 2021). Such substances are labile and allow a rapid recycling of organic matter. Given the limited terrestrial inputs, there appears to be a close connection between the more balanced auto- and heterotrophic processes and the cycling of autochthonous origin DOM in the Greiner watershed as has been seen in lakes in other northern regions (Bogard et al., 2019; Tank et al., 2011).

2.5.3 Drivers of lake metabolism and evidence of internal cycling

GPP was best explained by variables related to light, internal production, and nutrient cycling (TP, %C4, Irradiance $\bar{z}$). In contrast, TN in headwater lakes (mean ± SD, 870 ± 371 µg L^{-1}) was nearly 2.5 times higher than the average reported in ~1000 surveyed lakes from the Canadian Arctic (352 ± 366 µg L^{-1}; Dranga et al., 2018). As TN content greatly exceeded TP content, P limitation of autotrophic growth was likely, as evidenced in the high N:P ratios at all sites, particularly in headwater lakes. The shallow organic horizon (<10 cm) present in the Cambridge Bay area (Kim et al., 2021), in addition to the predominantly limestone bedrock (McLennan et al., 2018), rarely allows higher contents of P to leach from the bedrock as would happen in more organic rich soils (Hobbie et al., 1999). An earlier study of headwater lake ERA5 provided evidence of P-limitation and showed high TP concentrations facilitated an increase in cyanobacterial biovolume (Ayala-Borda et al., 2021). Therefore, P appears to be a limiting element in the landscape, and it is likely that P availability directly controls primary production in the lakes of southern Victoria Island.

As mentioned above, well-lit benthic mats are highly productive. They also have access to higher nutrient concentrations in interstitial waters and sediments (Bonilla et al., 2005), which promotes algal growth in the benthos that dominates lake metabolism (Karlsson et al., 2009). This further supports the evidence that GPP was fueled by an efficient internal cycling and recycling of C and nutrients, as has been noted for shallow boreal Alaskan lakes (Bogard et al., 2019).

In contrast, the most important drivers for ER were TP, Irradiance $\bar{z}$ and BP, indicating that ER is largely autotrophic, coupled with GPP and that nutrients are internally recycled. BP negatively affected ER likely because the highest values for bacterial production were registered in lakes with low ER rates (PND3 and PND5). Although BP is often related to higher respiration, its effect on autotrophy might be related to the internal recycling of OM as bacterial remineralization products including nutrients, C (Legendre & Rassoulzadegan, 1995), vitamins and micronutrients (Croft et al., 2005) are consumed by primary producers. In turn, the labile protein-like organic product of algal exudates (e.g., component C4) is more easily consumed and reincorporated into the food web through the microbial loop than less bioavailable substances (Panzenböck et al., 2000; Seymour et al., 2017). The close connection between bacteria and algae generates an efficient cycle of nutrients, and the readily usable organic matter allows shallow waterbodies to have a self-sustained metabolism resulting in equilibrium or at times, net autotrophy.

Wetland coverage appeared in some of the most plausible models and had a relatively high importance weight. The closer contact of small waterbodies with the surrounding organic soil allows C and nutrient exchange between compartments likely taking part in the ER budget (Casas-Ruiz et al., 2023). In contrast, higher evaporation rates during summer, as observed with d-excess values, promoted the increase in NEP in waterbodies rich in C and nutrients. Oligotrophic-autotrophic lakes at lower latitudes show similar patterns (Bogard & Del Giorgio, 2016), hence the negative effect on ER observed in this study.

We argue that, during the open water season, light penetration promotes productive benthic mats and higher content of autochthonous, labile organic matter, when coupled with internally recycled nutrients, interact to drive net ecosystem production in lakes of the Greiner Lake watershed. Importantly, we show a clear metabolic transition throughout the watershed. GPP exceeds ER in shallow headwater lakes rich in nutrients and C, but low in aromatic compound content, where depth enables light penetration. In contrast, ER vs. GPP was near equilibrium in larger, deeper, and highly connected midstream and downstream lakes with lower nutrient and C content, more aromatic organic matter and reduced benthic light exposure.

2.6 Implications

Over an annual cycle, the metabolic balance of lakes in the watershed may depend importantly on lake depth relative to the vertical extent of ice cover. Net heterotrophic metabolism may be more extensive in deep lakes that do not freeze to the bottom, as evidenced in winter samples from Greiner Lake in this study. Deeper lakes can continuously respire the organic matter from the catchment and that generated in the previous ice-free season in the water and the sediment (Saros et al., 2023). Conversely, low to no metabolic activity may exist in shallow (<2 m) and isolated lakes that freeze to the bottom in winter (Rautio et al., 2011), thereby limiting the breakdown of previously-fixed autochthonous organic matter and the extent of heterotrophy over the annual timescale. Open-water, net autotrophic predominance in our studied lakes demonstrates that the food webs of shallow Arctic lakes can impact regional C cycling by acting as C sinks during their short participation in landscape metabolism. These findings would not have been possible by measuring GHG content alone.

In the future, climatic change could affect lake metabolic states through lengthened ice-free periods and increases in migratory bird populations, both of which increase waterbody nutrient loadings (Luoto et al., 2014; McGowan et al., 2018), and ultimately increase primary production over longer summer periods (Smol et al., 2005). In addition to nutrients and extended growing seasons, climate driven terrestrial greening and forest development (McGowan et al., 2018) could enhance heterotrophic food web components and make longer-term metabolic trajectories more uncertain. Arid landscapes, similar to Southern Victoria Island, are prone to increased evapoconcentration (Smol & Douglas, 2007) and decreased runoff (Bouchard et al., 2013) that have potential consequences for the metabolism of local freshwater systems. The synergistic effects of higher temperatures and increased evaporation rates have already been documented in nearby geographical regions of Nunavut (Carroll & Loboda, 2018), and have led to higher nutrient concentrations that may result in waterbody eutrophication and negative ecosystem effects (Mariash et al., 2018a). The presence of eutrophic lake ERA5 (Ayala-Borda et al., 2021) shows the possible resulting effects of increasing P loads and the vulnerability of freshwater ecosystems in the Greiner Lake watershed. Such outcomes point to an uncertain future for Arctic lakes in low elevation arid regions of the Arctic such as southern Victoria Island.

2.7 Conclusions

This study demonstrates how lake metabolism is regulated by the combined influence of hydrology, light and internal nutrient cycling, which collectively determine the potential characteristics of Arctic lake food webs, located in arid, low elevation regions, and whether those lakes are sinks versus sources of CO_2 during the polar summer. These shallow lakes are sites of limited C mineralization that mostly depend on benthic primary production and internal recycled products to sustain metabolism. Lakes with low connectivity (i.e., headwaters) were rain fed but, contrary to predictions, had relatively low amounts of allochthonous OM and higher amounts of autochthonous OM and nutrients. They also had the highest GPP values and were mostly net autotrophic. In contrast, the more hydrologically-connected lakes (i.e., midstream and downstream) were not significantly different from lakes with a lower degree of connectivity, even though they had higher concentrations of aromatic, allochthonous material. However, the lower nutrient and C content, and reduced light penetration in deeper, highly connected, midstream, and downstream lakes led to lower rates of GPP and ER, and a more balanced metabolism near equilibrium. Measurements of DOM content and composition indicated that the dominant sources likely were internal microbial and algal communities, especially in headwater lakes, and revealed the importance of benthic mats and the microbial loop in the metabolism of many oligotrophic Arctic lakes. Although we found metabolic differences along the connectivity gradient, there was little effect on lake chemical composition from terrestrial DOM sources or permafrost degradation. Rather, we attributed the differences to high evaporation rates in shallow lakes with low connectivity, the higher volume of water diluting compounds in highly connected lakes and internal metabolic and abiotic processes. Our study, therefore, highlights the importance of shallow freshwater ecosystems in arid regions of the Arctic. Such systems are of particular importance due to their widespread occurrence on the landscape and their high rates of productivity that ultimately sustain watershed food webs. Given that these lakes represent the largest group of waterbodies in areas like Victoria Island, our results further underline the vulnerability of Arctic arid landscapes and their associated food webs to ongoing climate change.

2.8 Acknowledgements

This research is a contribution to the projects "Functional, structural and biodiversity studies of Arctic freshwater watersheds: validating protocols for monitoring and cumulative impacts assessment" and, "Health of Arctic freshwater ecosystems, and Changing nutrients and food web health in northern lakes and rivers", supported by the Natural Sciences and Engineering Research Council of Canada (NSERC), Polar Knowledge Canada, and ArcticNet, with logistic support from the Polar Continental Shelf Program (PCSP). P. Ayala-Borda was supported by the EcoLac NSERC-CREATE Program and Fonds de recherche du Québec – Nature et technologies (FRQNT). M. Bogard was financially supported by the Canada Research Chairs Program. We thank Pénélope Blackburn-Desbiens and Mathieu Archambault for their field and lab assistance, and Brent Else, Elise Imbeau, Gabriel Ferland and Frédéric Bouchard for their winter and spring isotope and gas sampling support. Finally, we thank Juliette Lapeyre for the satellite image processing.

2.9 Supplementary material

2.9.1 Supplementary methods

2.9.1.1. Dissolved CO_2 concentrations

To estimate the relative roles of NEP versus external sources of water in determining whether the studied lakes were sinks or sources of CO_2, samples for dissolved CO_2 concentration were taken from ten lakes from May to August. Water was sampled using a 2L Limnos water sampler and immediately transferred to 60 or 100 ml syringes. 30 ml of ambient air was introduced to the same syringe and then shaken vigorously for 3 min to reach equilibrium. The gas in the headspace was then transferred to pre-evacuated 12 ml Exetainer vials (Labco, United Kingdom) with airtight butyl rubber septa. Atmospheric air samples were also taken in separate tubes for every site. Samples were analyzed at the University of Lethbridge using a Thermo Trace 1310 gas chromatograph equipped with a methanizer and flame ionization detector and calibrated against known standards. Henry's Law was used to calculate CO_2 at equilibrium and CO_2 concentration in the water sample from headspace measurements. Results were compared with atmospheric CO_2 concentrations.

2.9.2 Supplementary figures

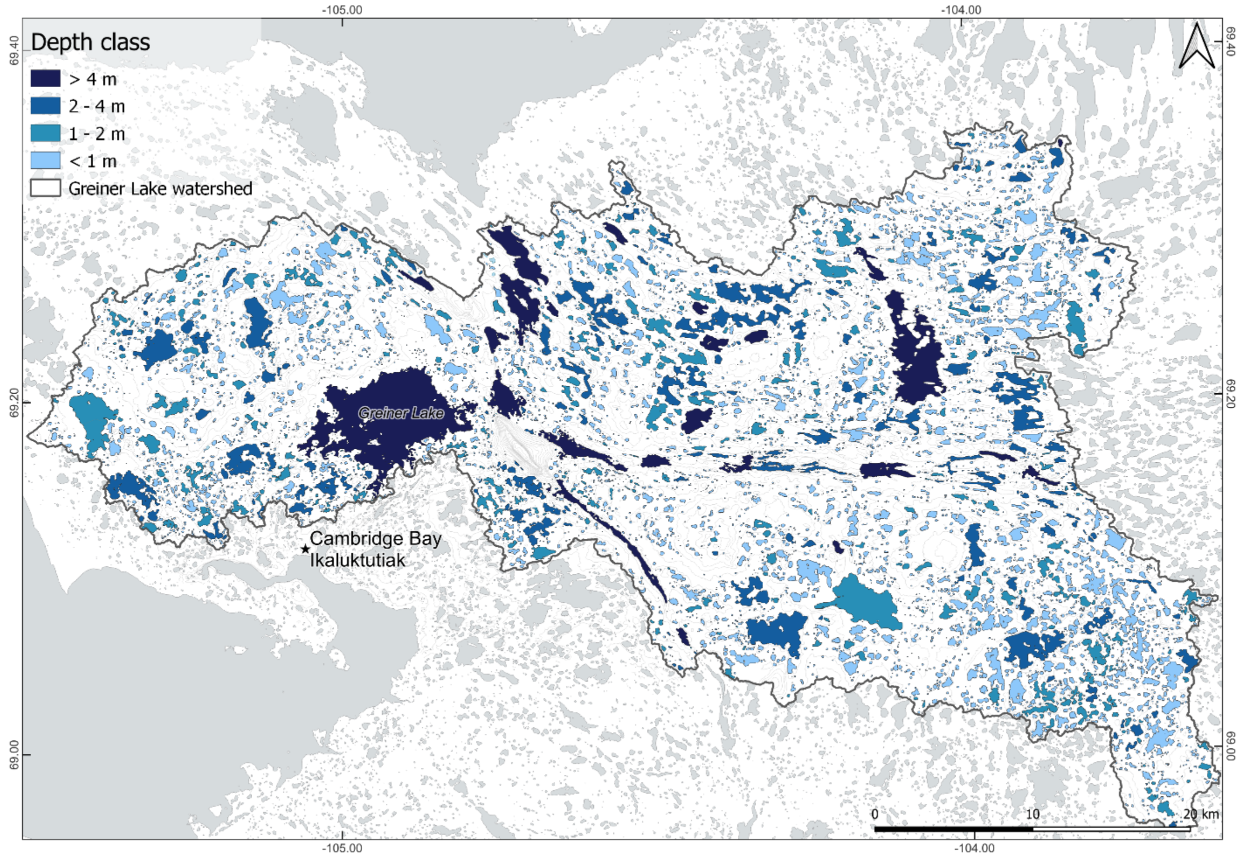


Figure S2. 1 Distribution of lakes in the Greiner Lake watershed according to depth class.

Figure S2. 2 . Oxygen saturation and temperature profiles for lakes sampled in a) 2018 and b) 2019. Values for VG4 are not available. Depth profiles were taken at the deepest possible point detected through inspection with a depth meter. The maximum operational depth of the RBR was 20 m. The solid line is oxygen saturation, and the dotted line is temperature. Note the different scales in the y-axis.

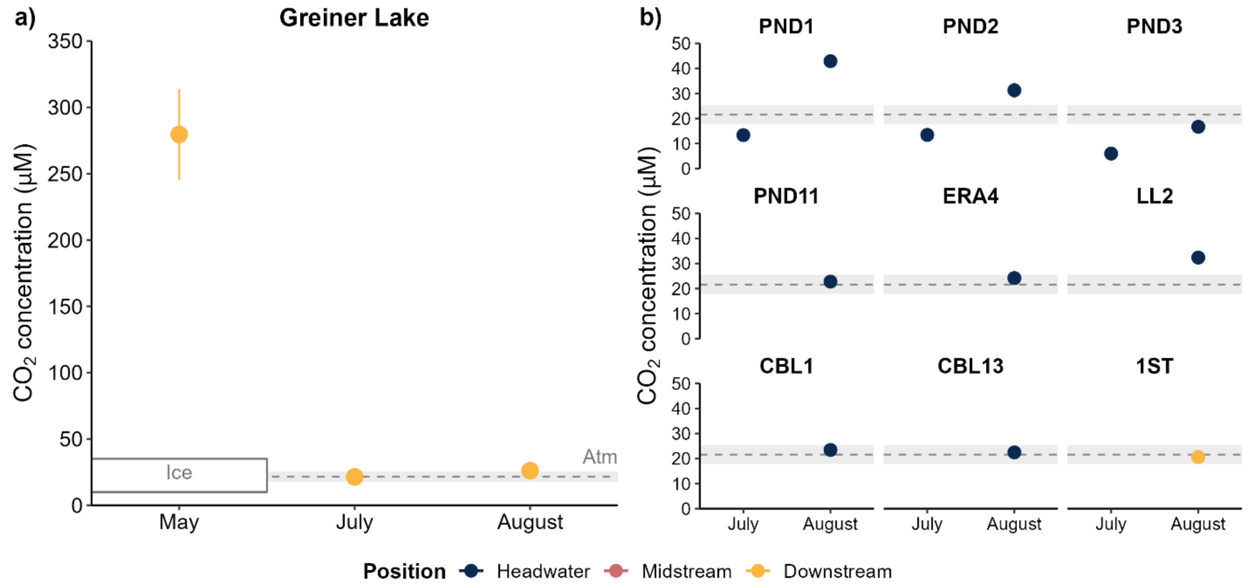


Figure S2. 3 CO$_2$ concentrations measured in May, July, and August 2022 for Greiner Lake (a) and July, August, or both in 2022 measured for 9 lakes (b). The dashed line and shaded area, respectively, indicate the average concentration ± one standard deviation of atmospheric CO$_2$ (21.6 ± 3.8). Note the different scales on the y-axis.

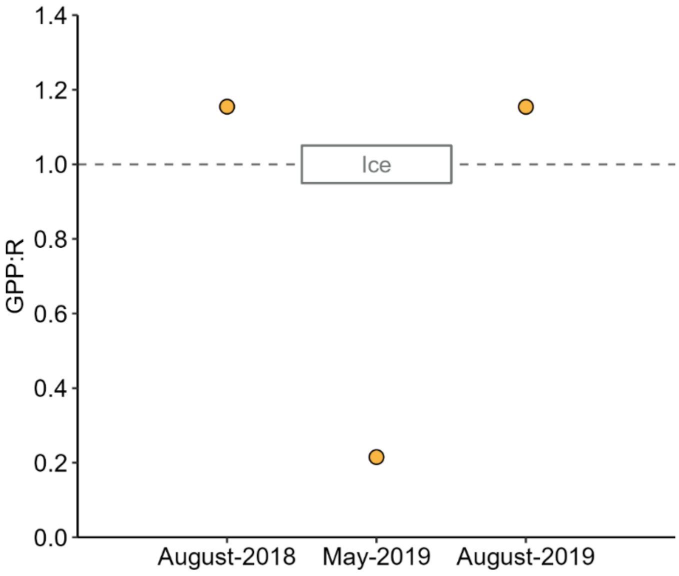


Figure S2. 4 GPP to R ratio for Greiner Lake in late winter 2019 compared to values found in summer 2018 and 2019. Values above the dashed line represent net autotrophy.

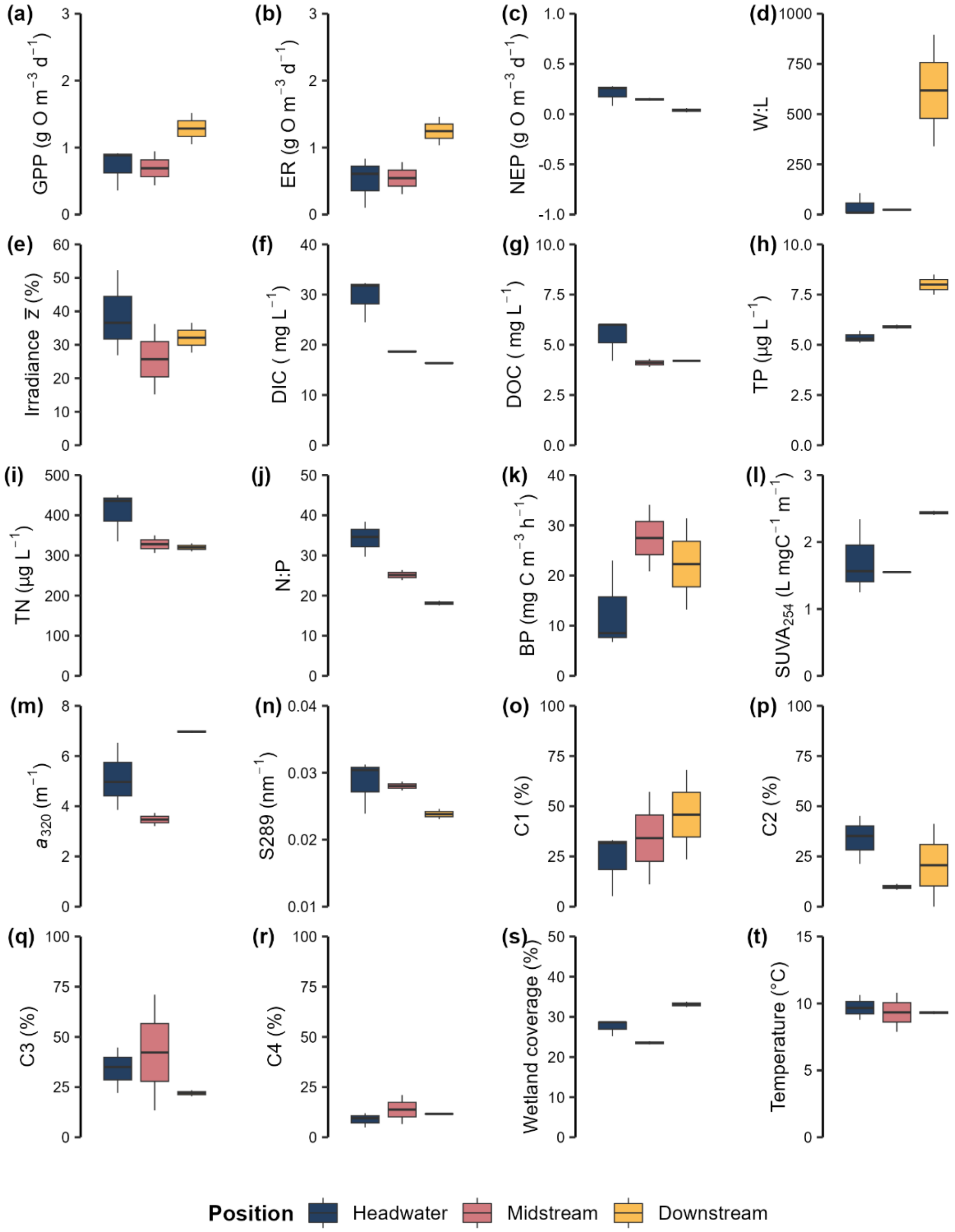


Figure S2. 5 Metabolic rates a) to c) and physicochemical variables d) to t) in a subset of lakes of similar depths in each category (i.e., between 4.8 and 12.1 m). Headwater lakes: CBL1, ERA4, Midstream lakes: CBL6, CBL7, Downstream lakes: CBL2, CBL19

2.9.3 Supplementary tables

Table S2. 1 PARAFAC component descriptions, fluorescence signatures and highest intensity excitation and emission peaks parenthesis.

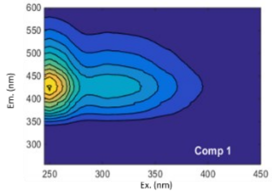
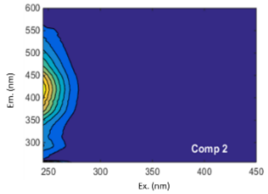
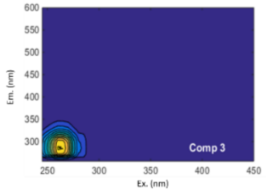
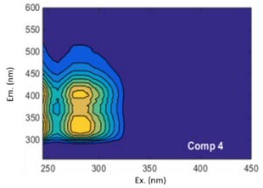
Component	**Fluorescence signatures**	**Excitation (nm)**	**Emission (nm)**	**Description**	**Reference**
C1		250	428	Humic like fluorophore[a] and terrestrial[b]	[a](Amaral et al., 2016; Graeber et al., 2012; Romero et al., 2019) [b](Painter et al., 2018; Stedmon & Markager, 2005)
C2		<245	416	Terrestrially derived product[c] Humic material[d]	[c](Amaral et al., 2020; Kothawala et al., 2014) [d](Murphy et al., 2006)
C3		260	284	Tyrosine–like organic matter[e] Combination of protein–like material, tannin like low molecular weight organic matter[f]	[e](D'Andrilli & McConnell, 2021) [f](D'Andrilli et al., 2017)
C4		<245/280	338/402	Tryptophan–like autochthonous microbial material[g]	[g](Andersson et al., 2018; Kothawala et al., 2012; Stedmon & Markager, 2005)

Table S2. 2 PARAFAC components for all sampled lakes in 2018 and 2019 in Raman units and percentages.

Lake	**Year**	**C1 (R.U.)**	**C2 (R.U.)**	**C3 (R.U.)**	**C4 (R.U.)**	**C1 (%)**	**C2 (%)**	**C3 (%)**	**C4 (%)**
1ST	2018	0.8	0.0	0.2	0.2	71	0	14	15
1ST	2019	1.5	28.1	12.6	2.6	3	63	28	6
2ND	2018	0.7	2.0	1.3	0.5	16	43	30	11
2ND	2019	0.5	0.6	0.6	0.2	26	32	30	12
CBL1	2018	0.5	0.3	0.5	0.2	32	21	35	12
CBL13	2018	1.0	0.2	10.0	0.5	9	2	86	4
CBL15	2018	2.4	98.6	29.5	4.7	2	73	22	3
CBL16	2018	0.6	0.0	0.2	0.1	66	0	18	16
CBL19	2018	0.7	0.0	0.2	0.1	68	0	20	12
CBL2	2018	0.6	1.0	0.6	0.3	24	41	23	12
CBL5	2018	0.8	0.6	1.3	0.2	26	21	45	8
CBL5	2019	0.7	1.1	0.8	0.3	25	38	26	11
CBL6	2018	0.6	0.6	4.1	0.4	11	11	71	7
CBL7	2019	0.6	0.1	0.1	0.2	57	8	13	21
ERA1	2018	0.9	2.8	8.3	0.9	7	21	65	7
ERA1	2019	0.5	0.5	0.9	0.3	24	23	40	13
ERA4	2018	0.7	0.8	0.5	0.2	33	35	22	10
ERA4	2019	1.2	10.4	10.3	1.1	5	45	45	5
ERA5	2018	1.2	5.2	9.2	0.9	7	32	56	5
GRL	2018	0.9	0.0	0.2	0.2	69	0	19	13
GRL	2019	0.9	0.1	5.9	1.5	10	1	70	19
LL1	2019	0.6	0.9	0.9	0.3	23	34	32	11
LL2	2019	0.0	106.4	77.5	10.2	0	55	40	5
VG1	2019	1.7	0.0	0.3	0.5	67	1	11	21
VG2	2019	2.0	1.0	3.1	1.3	27	13	42	18
VG3	2019	0.5	0.5	0.3	0.2	35	34	19	13
VG4	2019	1.1	0.1	2.1	1.1	24	2	47	26
VG5	2019	0.0	113.9	161.4	20.9	0	38	54	7
PND1	2018	0.3	0.4	0.5	0.2	25	26	34	15
PND10	2018	2.4	9.5	15.0	1.2	9	34	53	4
PND11	2019	0.4	0.0	1.7	0.4	15	1	67	16
PND12	2019	0.5	0.5	0.7	0.2	26	24	37	13
PND18	2019	0.8	0.0	0.1	0.1	78	0	6	15
PND2	2018	1.2	0.0	0.3	0.3	69	0	17	14
PND3	2019	1.1	0.6	5.5	0.8	14	7	69	10
PND4	2019	1.4	0.3	7.1	2.3	13	3	64	20
PND5	2019	0.4	16.0	20.3	5.0	1	38	49	12
PND6	2019	1.6	38.2	18.0	2.1	3	64	30	3
PND7	2019	0.4	0.0	0.1	0.1	69	0	14	17
PND8	2019	1.4	0.4	2.4	1.5	24	7	42	27
PND9	2019	0.4	0.0	0.1	0.2	52	4	18	27

Table S2. 3 Ranking of the best multiple linear regression models (based on lowest AICc) used to explain the differences in GPP and ER. Differences between each model and the best model AIC value (Δ AICi), the model proportion of explained variation (R^2), the Akaike model weight (w_i) and the cumulative Akaike weight (acc w_i).

Response variable	**#**	***Model***	***Δ AICi***	***R^2***	***w_i***	***acc w_i***
GPP	1	GPP ~ TP + C4 + Irradiance $\bar{z}$	0.00	0.71	0.19	0.19
	2	GPP ~ S_{289} + TP + C4 + Irradiance $\bar{z}$	0.37	0.72	0.16	0.35
	3	GPP ~ TP – BP + C4 + Irradiance $\bar{z}$	1.39	0.71	0.09	0.44
	4	GPP ~ S_{289} + TP – BP + C4 + Irradiance $\bar{z}$	1.61	0.73	0.08	0.53
	5	GPP ~ TP + C4 + Irradiance $\bar{z}$ – d-excess	2.19	0.71	0.06	0.59
	6	GPP ~ TP + C4 – $SUVA_{254}$ + Irradiance $\bar{z}$	2.30	0.71	0.06	0.65
	7	GPP ~ TP + C4 – W:L + Irradiance $\bar{z}$	2.43	0.71	0.06	0.70
	8	GPP ~ S_{289} + TP + C1 + C4 + Irradiance $\bar{z}$	2.51	0.72	0.05	0.76
	9	GPP ~ TP + C4 – Upstream lakes + Irradiance $\bar{z}$	2.53	0.70	0.05	0.81
	10	GPP ~ TP + C1 + C4 + Irradiance $\bar{z}$	2.57	0.70	0.05	0.86
	11	GPP ~ TP – C3 + C4 + Irradiance $\bar{z}$	2.67	0.70	0.05	0.91
	12	GPP ~ S_{289} + TP – C3 + C4 + Irradiance $\bar{z}$	2.94	0.72	0.04	0.96
	13	GPP ~ S_{289} + TP + C4 + Irradiance $\bar{z}$ – d-excess	2.99	0.72	0.04	1.00
ER	1	R ~ TP – BP + Wetland + Irradiance $\bar{z}$ – d-excess	0.00	0.53	0.13	0.13
	2	R ~ TP – BP + C4 + Irradiance $\bar{z}$	0.10	0.50	0.13	0.26
	3	R ~ TP – BP + Irradiance $\bar{z}$	0.20	0.47	0.12	0.38
	4	R ~ TP – BP + Wetland + Irradiance $\bar{z}$	0.52	0.49	0.10	0.48
	5	R ~ TP– BP + C1 + Irradiance $\bar{z}$	0.67	0.49	0.10	0.58
	6	R ~ TP – BP – C2 + Irradiance $\bar{z}$	1.54	0.48	0.06	0.64
	7	R ~ TP – BP + C4 + $SUVA_{254}$ + Irradiance $\bar{z}$	1.77	0.51	0.06	0.70
	8	R ~ TP + C1 + Irradiance $\bar{z}$	1.81	0.44	0.05	0.75
	9	R ~ TP – BP + C4 + Wetland + Irradiance $\bar{z}$	1.83	0.51	0.05	0.80
	10	R ~ TP – BP – C3 + Irradiance $\bar{z}$	1.84	0.47	0.05	0.86
	11	R ~ TP – BP + C1 + Wetland + Irradiance $\bar{z}$	1.91	0.51	0.05	0.91
	12	R ~ TP – BP – C2 + Wetland + Irradiance $\bar{z}$ – d-excess	2.13	0.54	0.05	0.95
	13	R ~ TP – BP + Upstream lakes + Irradiance $\bar{z}$	2.14	0.47	0.05	1.00

CHAPTER 3 CARBON TRANSFER

Insights into the influence of lake depth and microbial eukaryotic plankton composition for polyunsaturated fatty acids in zooplankton of Arctic lakes

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Keywords: Arctic lakes, polyunsaturated fatty acids, zooplankton, microbial eukaryotes, pelagic food web, climate vulnerabilities

3.1 Abstract

Rapid global warming is affecting the Arctic and is being reflected in freshwater ecosystems, producing changes in the physical, chemical, and biological composition of the water. Increasing nutrient content, greater allochthonous carbon and changes in light availability are the most commonly observed changes affecting lake ecosystems. Shallow Arctic lakes exposed to high evaporation rates are especially vulnerable to these changes in the short term, but basic knowledge of these sentinels of climate change is lacking. Primary and secondary consumers rely on primary producers and other microbial eukaryotes for essential fatty acids, but changes in the composition of the lower levels of the planktonic community can affect the quality of food webs within lakes. Here, we analyzed microbial eukaryotic plankton community composition, linking it to the polyunsaturated fatty acid (PUFA) profiles of the zooplankton in lakes within the Greiner Lake watershed of southern Victoria Island, Nunavut (Canada). We compared PUFA in particulate material in lakes along a depth gradient to determine the sources of PUFA in resident zooplankton. Our results indicate that zooplankton diet in deep lakes is strictly pelagic and rich in docosahexaenoic acid (22:6n3) due to the high availability of dinoflagellates. Contrastingly, zooplankton in shallow lakes have lower PUFA content and depend more on a mix of pelagic and benthic sources rich in diatoms and cryptomonads. Results for these Arctic lakes emphasize the importance of planktonic high quality food sources for consumers in deep lakes and highlight the vulnerability of food webs in shallow Arctic lake food webs to ongoing climate change.

3.2 Introduction

The rate of warming in the Arctic is driving significant changes in freshwater ecosystems notably in diminished ice cover thickness and duration altering the phenology of the organisms living in these waters (Post et al., 2019). In Arctic lakes both pelagic and benthic production can occur, with benthic communities often contributing the bulk of algal production (Rautio & Vincent, 2006). This can be especially the case of small shallow lakes that constitute the most abundant type of lakes in the Arctic (Downing et al., 2006) and where primary production is dominated by the benthos (Cazzanelli et al., 2012). As there are differences in the quality and concentration of fatty acids in the two types of algal primary producers, the balance between benthic and pelagic production has consequences for the health and nutritional quality of Arctic charr (*Salvelinus alpinus*) and Lake whitefish (*Coregonus clupeaformis*), which are a major dietary staple in northern communities (Sharma et al., 2010). The fish do not directly feed on the algae or small protists but rely on zooplankton and other small invertebrates that do. In particular, zooplankton are not able to synthesize essential fatty acids and comparisons of essential dietary fatty acids in these primary consumers feeding on pelagic versus benthic algae in Arctic lakes and ponds has not been extensively studied.

Zooplankton are a key component in the diet of small and juvenile fish, that are ultimately consumed by larger fish (adults) and people (Power et al., 2009; Richardson et al., 2001). They also constitute one of the main sources of polyunsaturated fatty acids (PUFAs) found in higher lake trophic levels (Kainz et al., 2004). PUFA are a subset of fatty acids that are synthesized almost exclusively by primary producers and essential for consumers incapable of synthesizing PUFA (i.e., fish; Guschina & Harwood, 2009). PUFA are important constituents of cell membranes and are involved in the growth, development, reproduction and other critical functions

(Brett & Müller-Navarra, 1997). In cold regions, PUFA can serve as an energy store for overwintering zooplankton and fish, enabling survival during periods when primary production is minimal or absent (Grosbois et al., 2017; Mariash et al., 2017). PUFA content, however, is not uniform among algal taxa and, therefore, habitat related differences in PUFA availability and differences in the PUFA content of grazers and predators with differing feeding strategies (Grosbois et al., 2022; Hiltunen et al., 2015). Some freshwater phytoplankton taxa are richer in PUFA than others, especially for eicosapentaenoic acid (EPA, 20:5n3) and docosahexaenoic acid (DHA, 22:6n3) (Taipale et al., 2013). The most common PUFA-rich groups are diatoms, dinoflagellates, and cryptophytes (Taipale et al., 2013; Yan et al., 2023) and are preferred by certain zooplankton when available (Cowles et al., 1988). Benthic algae may also be sources of PUFA for zooplankton but may contain less PUFA per unit volume. However, the overwhelmingly high biomass of benthic mats, and the benthic feeding mode of many zooplankton in shallow Arctic lakes makes benthic primary producers a key source of PUFA to certain zooplankton (Mariash et al., 2014). While specific PUFA-rich phytoplankton groups and zooplankton ingestion are largely studied in laboratory-based experiments (e.g., Peltomaa et al., 2017), the links between sources and consumers are less understood in nature due to the lack of identification of planktonic organisms and their role in the food web.

While predator-prey and proportional prey reliance relationships can be determined using bulk stable isotope methods (Middelburg, 2014), the origin of energy sources, such as PUFA, are not suited to the method unless more sophisticated fatty acid–specific stable isotope analyses are also used, such as δ^2H in combination with δ^{13}C (Pilecky et al., 2021). Furthermore, determining the specific composition of any diet can be challenging when the benthic and pelagic algal communities are unknown (Majdi et al., 2019). Although modelling is often used based on a "consumer-resource library" of fatty acid signatures (e.g., Strandberg et al., 2015) or a combination of various techniques to estimate the major food source algal groups (e.g., Peltomaa et al., 2023). However, as long as the planktonic species of a lake remain unknown, determining food sources for zooplankton will be restricted to a few already studied food sources, potentially leaving out species-species or environment-species interactions. In consequence, environmental DNA (eDNA) sequencing and/or microscopic identification provide information on algal species with higher resolution (Johnson & Martiny, 2015; Pringle & Hutchinson, 2020). The use of high-throughput amplicon sequencing of the 18S rDNA gene for microbial eukaryote identification (i.e., autotrophic, heterotrophic and mixotrophic eukaryotes) quickly provides eukaryotic diversity information of a larger number of samples and sometimes at lower costs than traditional microscopy methods (Stein et al., 2014). This technique has gained popularity in freshwater ecology studies in recent years (Lopes Dos Santos et al., 2022), offering new avenues for the study of potential PUFA sources for zooplankton and the rest of the food web in understudied Arctic freshwater systems.

As the Arctic continues to experience increases in temperature, changes in the composition and phenology of algal communities are expected to occur, further exacerbating the structural and dynamic changes in food webs that have occurred to date (Quinlan et al., 2005; Saros et al., 2023). Communities of shallow lakes are particularly susceptible as smaller volume implies quicker and more intense warming and greater evaporation loss (Smol & Douglas, 2007) affecting not only the chemical composition of the water (Johnston et al., 2020), but also disrupting hydrological connectivity and shaping species composition in Arctic lakes (Blackburn-Desbiens et al., 2023). Community behavior could be altered, as mesotrophic species benefit from warmer temperatures with consequential changes in herbivore feeding habits, as reported in lower latitude lakes

(Devkota et al., 2022). Differences in temperature and productivity in subarctic lakes have similarly shown to affect the food web structure and PUFA content, with fastest responses taking place at lower trophic levels (Keva et al., 2021). In particular, as lakes become less clear with more CDOM and increased turbidity they may lose their benthic pathways forcing shallow lake zooplankton to switch primary food sources from benthic to pelagic algae (Mariash et al., 2018a). Given the relevance of zooplankton diets for ecosystem ecology and functioning, and the central role zooplankton play in supporting fish populations (Sterner, 2009), knowledge of zooplankton diets and how they may change is essential in the face of climate change.

To address questions regarding sources of PUFA in Arctic freshwater zooplankton, we sampled 35 lakes of the Greiner Lake watershed, located in the south of Victoria Island (Nunavut, Canada; Figure 3.1a and 3.1b), where most lakes are small and shallow (i.e.,<5 ha and <1 m) and lake metabolic pathways are highly dependent on benthic algae (Ayala-Borda et al., 2024a). We first used stable isotopes ($\delta^{13}C$ and $\delta^{15}N$) to estimate the dependence of zooplankton on potential organic carbon sources, focusing particularly on copepods and cladocerans that constitute the main mesozooplankton in lakes (Blackburn-Desbiens et al., 2023). Second, we measured the PUFA content of zooplankton food sources, including seston (pelagic) and benthic mats. The information was then used to estimate differences in resource quality within sampled lake types or habitats. Finally, concentrating on the pelagic lake food webs we determined the relative microbial eukaryote composition and distribution using 18S rDNA amplicons. Overall, we hypothesized that the variability in zooplankton diets would be reflected in differences in their PUFA content in different lakes and dependent on the area-volume properties of the lakes. To test this, we sampled a variety of lakes differing in benthic and pelagic production, chemical composition and depth: <1m (13 lakes), 1 to 10m (14 lakes) and >10m (8 lakes). We further hypothesized that: a) zooplankton in shallow lakes would depend more on benthic and terrestrial carbon sources and show poorer nutritional status compared to zooplankton in deeper and larger lakes; b) zooplankton in deep lakes would depend more on planktonic food sources and have higher PUFA content; and, c) the microbial eukaryotic community providing the largest share of PUFA to zooplankton would be dominated by diatoms, cryptophytes, and dinoflagellates, which are rich in these substances (Galloway et al., 2014).

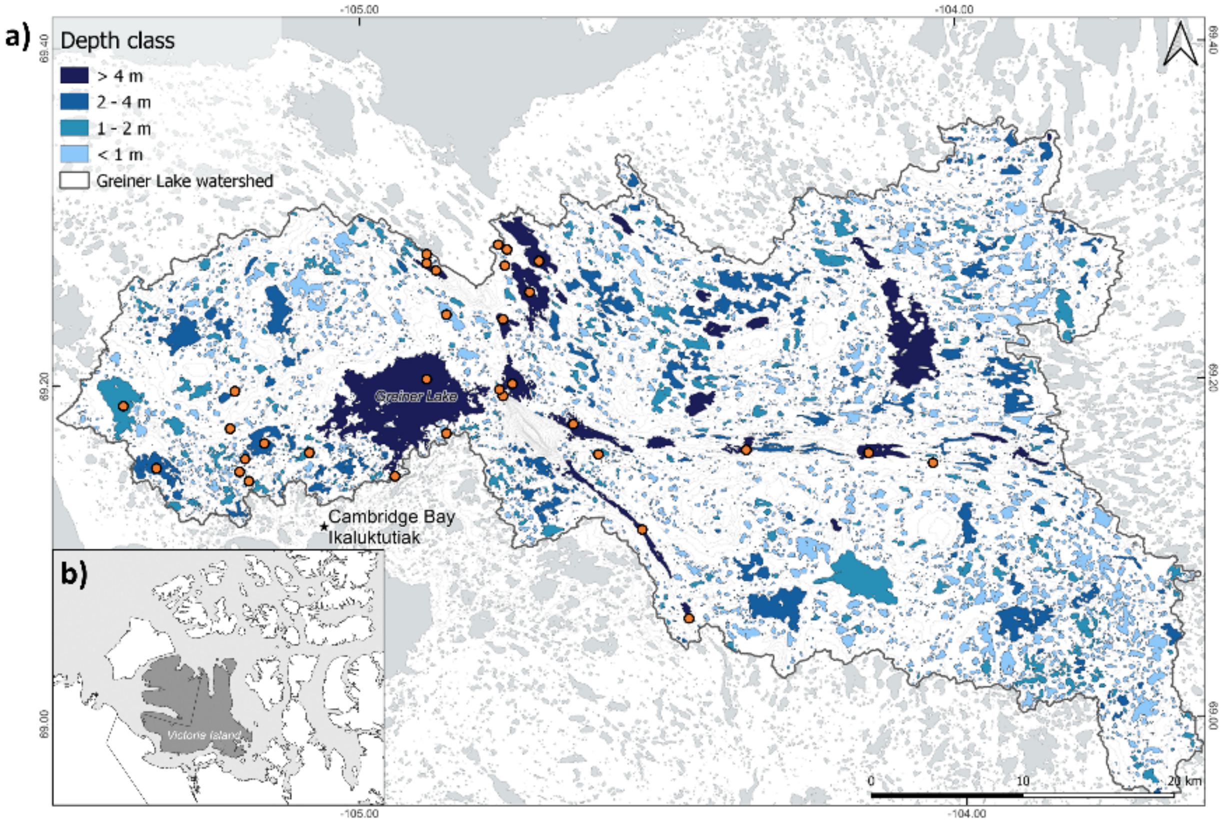

Figure 3. 1 a) Map of the sampling site close to Cambridge Bay, Nunavut with lakes classified according to depth b) view of Victoria Island in the Canadian Arctic Archipelago.

3.3 Methods

3.3.1 Site description and sampling

We sampled 35 lakes in the Greiner Lake watershed (69°10’35.72” N, 104°55’54.87” W) near Cambridge Bay, Nunavut (Figure 3.1a and 3.1b) in August 2018 and 2019. Six of these lakes (GRL, 1ST, 2ND, CBL5, ERA1 and ERA4) were sampled both years, giving a total of 41 observations. Lake depth, chemical composition of the water and water column profiles were previously published (Ayala-Borda et al., 2024a), with data available in Ayala-Borda et al. (2024b). Results of dissolved organic carbon (DOC), dissolved inorganic carbon (DIC), total phosphorus (TP), chlorophyll *a* (Chl *a*), the absorption coefficient at 440 nm (a_{440}) and the spectral slope between 279-299 nm (S_{289}) were used as descriptive variables of terrestrial carbon content, nutrients and algal production variability across the sites. Chl *a* was converted from units per volume to units per area, using lake mean depth.

Four liters of water from each lake were collected and sieved with 50 µm plankton nets to remove zooplankton from the samples. Samples for environmental DNA (eDNA) were sequentially filtered through 3-µm pore size 47-mm diameter polycarbonate filters placed into 2 ml microtubes. RNA*later*™ (1.5 ml; Thermo Fisher Scientific) was added to the microtubes followed by storage at -80 °C until extraction.

Seston samples from all lakes were filtered in duplicate for stable isotope ($\delta^{13}C$ and $\delta^{15}N$) and fatty acid analyses. Water was filtered through pre-weighed, pre-combusted GF/F filters and then freeze dried before further analysis. Bulk zooplankton samples were taken using a 30 cm diameter, 200 µm plankton net and sorted into copepods and cladocerans when possible. Rocks from the littoral zone were collected from all lakes to sample benthic mats. The mat material was dislodged from the rocks using an electric toothbrush (surface 0.79 cm^2, 10 mm diameter). Triplicates of zooplankton, seston and benthic mats were stored in Eppendorf tubes at -80 °C until freeze-dried for fatty acid and isotope analyses.

For comparison with the lake samples, terrestrial vegetation was collected from around the lake, pooling different species into one bulk sample. Soil was collected close to each lake with a small shovel, no further than 10 meters from the shore. Both terrestrial vegetation and soil samples were kept at -20 °C and then freeze dried for fatty acid analysis or dried at 60 °C overnight for stable isotope analysis.

3.3.2 Stable isotope and fatty acid analyses

Benthic mats and soil samples for $\delta^{13}C$ and $\delta^{15}N$ stable isotope analyses were first treated using acid fumigation to remove inorganic carbon from the samples. Samples were exposed to acidic fumes (100 ml of 12M HCl evaporating in a closed environment) for 10 hours for each 100 mg of sample (Ramnarine et al., 2011). Samples were allowed to evaporate after fumigation for 24 hours and were then re-dried at 60 °C. Benthic mats, vegetation, soil and zooplankton samples were analyzed and quantified for $\delta^{13}C$ and $\delta^{15}N$ at the Environmental Isotope Laboratory, Waterloo (ON, Canada), using a 4010 Elemental Analyzer (Costech Instruments, Italy) coupled to a Delta Plus XL (Thermo-Finnigan, Germany) continuous flow isotope ratio mass spectrometer. Seston filters were analyzed at the Stable Isotopes in Nature Laboratory, Fredericton (NB, Canada), using a NC2500 elemental analyzer coupled with a DELTA V Plus continuous flow isotope ratio mass spectrometer (Thermo-Finnigan, Germany). Results were reported in delta value per mil (‰), where $\delta^{13}C$ values were corrected against Vienna Pee Dee Belemnite (VPDB) and $\delta^{15}N$ were corrected with reference scale of Atmospheric air.

Fatty acids from freeze dried seston filters, benthic mats and zooplankton were weighed using a micro-balance (XP26 Delta Range, Mettler Toledo, Greifensee, Switzerland). Extraction and methylation were done with a chloroform-methanol mixture. Identification and quantification were completed using gas chromatography coupled with mass spectrometry (GC-MS) and internal standard curves as described in (Grosbois et al., 2017).

Phytoplankton $\delta^{13}C$ values were obtained from the average of algal specific fatty acids (18:4n-3, 20:1n-9, 20:5n-3 and 22:6n-3; Taipale et al., 2015b) extracted from seston in Greiner Lake published by Grosbois et al. (2022). $\delta^{15}N$ values were assumed to be the same as the average and standard deviation of the seston $\delta^{15}N$ isotopes in this study.

3.3.3 DNA extraction and sequencing

The eDNA was extracted using AllPrep DNA/RNA Mini kit (Qiagen, Hilden, Germany). The V4 region of 18S was amplified to construct libraries, using eukaryote E572F-E1009R (Comeau et al., 2016) universal primers. Amplicons were purified and tagged for multiplexing using specific linking MiSeq® primers. Amplicons were pooled in equimolar concentrations and sequenced by the "Plateforme d'Analyses Génomiques" (IBIS, Université Laval, Canada).

3.3.4 Sequence processing and data analyses

Overlapping paired end reads from the fastq files, primer removal, denoising, merging and chimera removal were processed using the DADA2 package (Callahan et al., 2016). Taxonomy was assigned to each amplicon sequencing variants (ASV) using PR2 v5.0.0 (Guillou et al., 2013). Large metazoans, prokaryotes and fungi were filtered from the eukaryotic ASV table using the *Phyloseq* package. ASV below the 1×10^{-5} threshold of relative abundance were also removed. For relevant taxa, taxonomy was refined by BLASTn against the NCBI database. PND2 showed a dominance (~70%) of Choanoflagellida and low presence of other phyla. We attribute this result to an error during filtration. This sample was excluded from the analyses in further steps.

Lakes were grouped in three depth categories according to the maximum recorded depth: < 1 m, 1-10 m, and > 10 m. As the stable isotope signatures of primary producers may vary between lake ecosystems as a result of variations in nutrient inputs, anthropogenic or other natural causes (Cabana & Rasmussen, 1996; Kline et al., 1993; Vander Zanden et al., 1997), testing of the differences among baselines is required. Here we used the seston $\delta^{15}N$ stable isotope samples from lakes in each lake depth group to compute a mean baseline value for the depth group and tested for significant differences among groups using ANOVA, after ensuring conformance to the homogeneity of variance assumption (Levene's test ($P > 0.166$). As differences among lake depth groups were significant (ANOVA $p < 0.001$), baseline adjustment was required. Adjustment was completed by computing the difference between the lake group baseline mean and the relevant $\delta^{15}N$ values for samples from each lake depth group. The difference values were then used in subsequent statistical testing that compared lake depth groups.

One-way ANOVAs were performed for PUFA (sum of C18.3n3, C20.3n3, C20.5n3, C22.6n3, C18.4n3, C18.2n6, C18.3n6, C20.2n6, C20.3n6, C20.4n6 and C22.2n6) comparisons among lake categories using the *ade4* package. Principal Component Analysis (PCA) for physicochemical variables, non-metric multidimensional scaling (NMDS) for microbial communities and fitting of zooplankton fatty acid or phyla vectors to the unicellular eukaryotic community NMDS with vegan and *phyloseq* packages. Multiple linear regressions (MLR) were performed using the *MuMin* library in R to determine the major microbial eukaryotic groups influencing zooplankton PUFA content. The best models were selected using the lowest Aikaike Information Criterion corrected for sample size (AICc). Akaike weights (w_i) of the models in which explanatory variable occurred were used to calculate variable importance weights (Σw_i) for the variable following (Symonds & Moussalli, 2010). Figures were produced using *ggplot2*. All analyses were completed using R v 4.2.1 (R Core Team, 2021).

3.4 Results

3.4.1 Water composition

Differences in the chemical composition of water along the connectivity gradient in the Greiner Lake watershed were seen in the PCA (Figure 3.2). PC1 and PC2 represent 75.1% of the variation in the data matrix. PC1 explained 49.7% of the variation and was mostly associated with DOC and DIC, while Chl *a* with TP and a_{440} were related to this axis to a smaller extent. PC2, explained 25.4% of the variation and was associated with S_{289}. Shallow lakes (i.e., <1 m deep) showed more variability and dispersion. Most had higher content of DOC, DIC and TP. Some lakes <1 m had higher terrigenous content (a_{440}), while others, with a few 1-10 m lakes were more associated with S_{289}, an indicator for dissolved organic matter of algal origin. Lakes >10 m depth were associated with higher Chl *a.* All deep lakes (i.e., >1m) had lower content of terrigenous indicators, but the content of Chl *a* per unit of area drove differences between lakes >10 m and all other lakes.

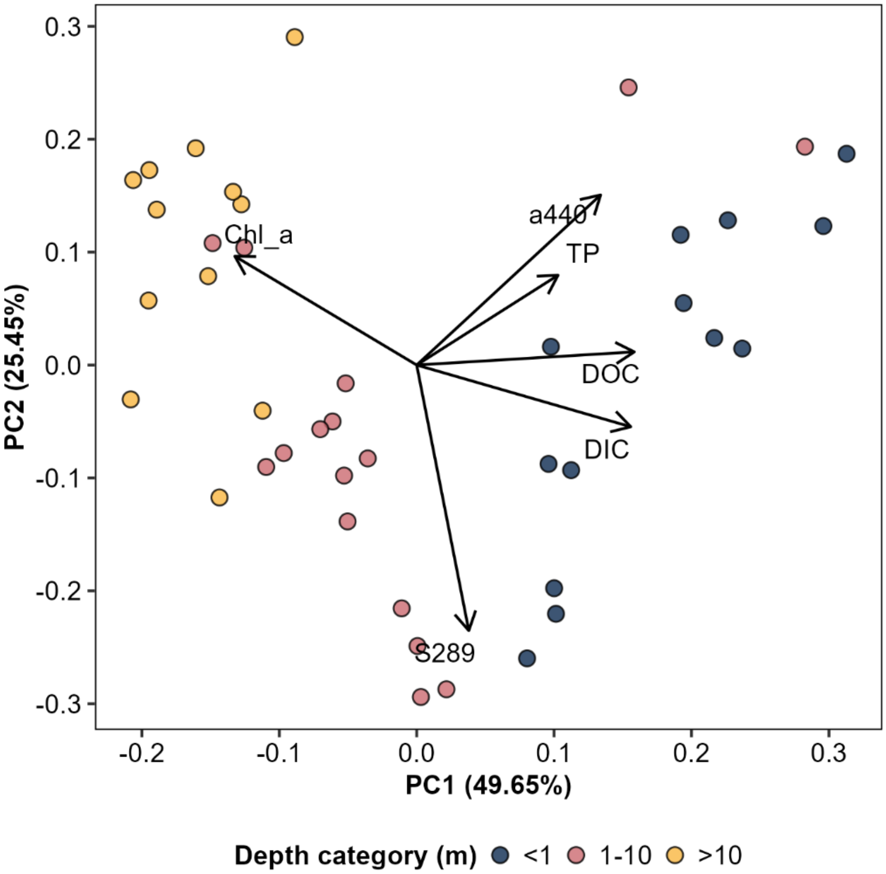

Figure 3. 2 Principal component analysis of all sites and descriptive chemical variables obtained from (Ayala-Borda et al., 2024b).

3.4.2 Stable isotopes

Stable isotope values of bulk zooplankton varied in the lakes, with shallow lakes having zooplankton with the highest δ^{13}C values (mean ± SD, -24.4 ± 2.6‰) and the lowest δ^{15}N values (2.8 ± 1.7 ‰). In contrast, the δ^{13}C values of zooplankton were lower and their δ^{15}N values higher in lakes 1-10 m deep (δ^{13}C: -28.4 ± 2.8‰, δ^{15}N: 5.6 ± 1.7‰) and lakes >10 m deep (δ^{13}C: -32.5 ± 1.8‰, δ^{15}N: 8.0 ± 0.6‰; Figure 3.3). The zooplankton community biomass, previously described by Blackburn-Desbiens et al. (2023), varies among lakes. Their data adapted to the depth categories in this study indicate that lakes >10 m had significantly higher biomass of copepods and significantly lower biomass of Cladocerans than the rest of the lakes ($p < 0.05$). Rotifera were assumed to have a minor impact on the zooplankton stable isotope values given the 200 µm net used for sampling did not show significant differences among the three lake depth categories (Figure S3.2). Lakes where the zooplankton community was dominated by copepods (i.e., lakes >10 m) had lower $\delta^{13}C$ values (-34.6 to -29.3), while lakes that were dominated by cladocerans (i.e., lakes <1 m) had zooplankton with higher $\delta^{13}C$ values (-28.7 to -20.0). Overall, zooplankton $\delta^{13}C$ values from lakes < 1 m overlapped with soil and seston $\delta^{13}C$ values and were the closest to benthic $\delta^{13}C$ of all zooplankton communities (Figure S3.3a and b). In deeper lakes zooplankton overlapped with either seston or phytoplankton $\delta^{13}C$ values, and the deepest lakes had higher baseline corrected $\delta^{15}N$ values than the putative diet sources, although $\delta^{15}N$ was only significantly high in >10m depth lakes as compared to <1m depth lakes (KW, $p < 0.05$). Additionally, zooplankton $\delta^{13}C$ showed a significant negative relationship with lake depth ($p < 0.001$, $R^2 = 0.49$) and was also significantly different among all depth categories (ANOVA, $p < 0.001$).

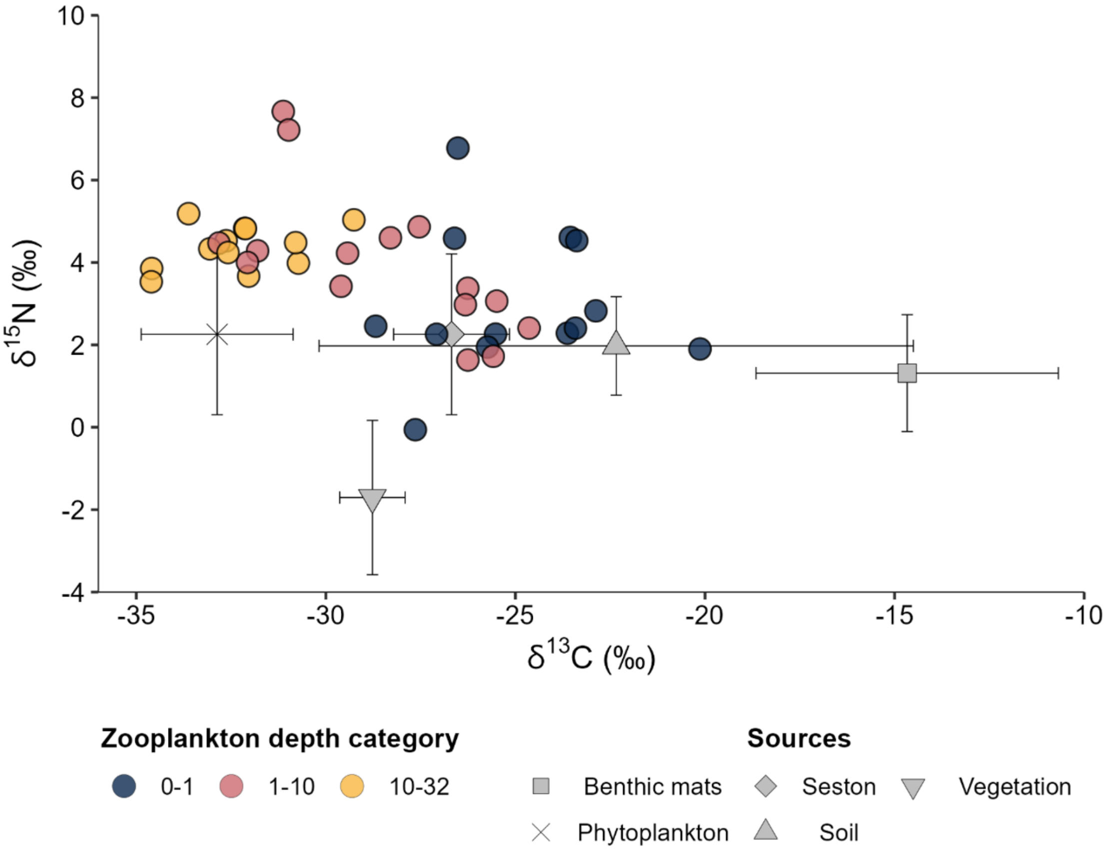

Figure 3. 3 Baseline corrected stable isotope values of zooplankton in each studied lake and potential carbon sources with standard deviation bars. Phytoplankton $\delta^{13}C$ values were obtained from compound specific isotopes of phytoplankton from Grosbois et al. (2022) and phytoplankton $\delta^{15}N$ values were assumed to be the same as seston in this study.

3.4.3 Fatty acids

PUFA content in seston per dry weight (DW) ranged from 0.4 to 7.1 µg mg^{-1} DW with significantly higher values in both the deeper lake categories compared to lakes < 1 m (Figure 3.4). PUFA in benthic mats ranged from 0.3 to 7.6 µg mg^{-1} DW, with no significant differences among depth categories (Figure 3.4). PUFA content per mg DW was significantly higher in seston compared to benthic mats (t-test, $p < 0.01$). Significantly higher concentrations of PUFA were found in zooplankton compared to seston and benthic mats (ANOVA, $p < 0.01$), with values ranging from

45.5 to 241.0 μg mg^{-1} DW. When PUFA in the different lake depth categories were compared, zooplankton in the lakes deeper than 1 m had significantly higher concentrations than zooplankton in lakes < 1 m (ANOVA, $p < 0.01$; Figure 3.4).

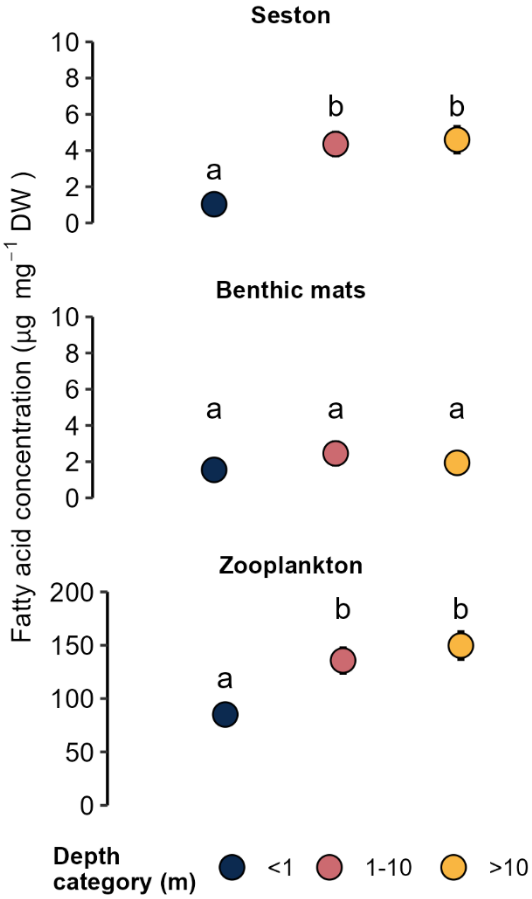

Figure 3. 4 The average polyunsaturated fatty acid content and standard error of seston, benthic mats and zooplankton in the three lake depth categories. Note the difference in the y axis. Different letters denote significant differences between groups at the α=0.05 level of significance.

3.4.4 Eukaryotic microbial community as zooplankton PUFA source

A total of 1378048 reads were recovered from the > 3 µm fraction of the 35 lakes (41 libraries), grouped in 4528 amplicon sequence variants (ASV). Species richness was similar among lakes except for PND8 where the number of ASV was below 40 compared to the average of 128 ASV. In shallow <1 m depth lakes the composition of the microbial eukaryotic community was variable, with a few lakes dominated by >60 % of Chrysophycea, while other lakes were dominated by Ciliates and Cryptophyceae. Chlorophyceae was present in higher proportions in lakes in the <1 m grouping and was one of the major drivers separating the depth categories (Figure 3.5 and S3.4). In lakes >1 m depth, the microbial eukaryote community had similar proportions of Chrysophyceae, Ciliates, and Cryptophyceae, whereas the proportion of Dinophyceae was higher in these lakes than in the <1 m depth lakes (Figure S3.4). Deep lakes also differed from shallow lakes in terms of the proportional presence of the heterotrophic lineage Kathablepharidea and mixotrophic lineage Dinophyceae that contributed most to the variation (Figure 3.5). Both Dinophyceae and Kathablepharidea were significantly correlated with lake depth (Figure S3.5).

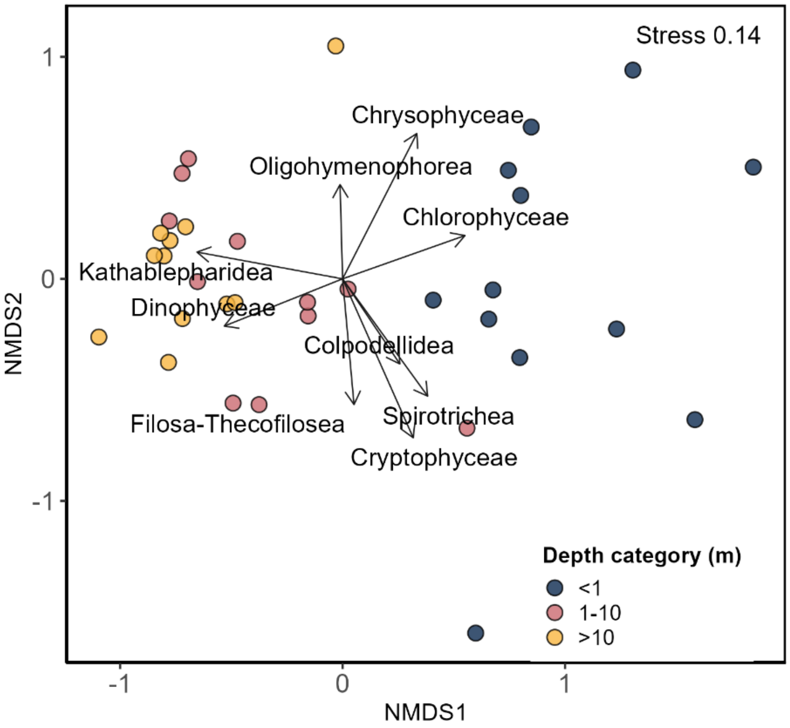

Figure 3. 5 Non-metric multidimensional scaling of microbial eukaryotes (>3 µm) with vectors of significant phytoplankton orders ($p < 0.05$).

Zooplankton in lakes with higher relative proportions of Dinophyceae and Cryptophyceae, combined or alone, showed higher proportions of DHA and C22:2n6 (Figure 3.6). Zooplankton in lakes where the microbial eukaryotic plankton community had a low relative proportion of Dinophyceae and Cryptophyceae had the lowest proportion of DHA regardless of the zooplankton composition. The lowest DHA proportions were found in shallow <1 m deep lakes (Figure S3.6). Zooplankton in >1 m depth lakes had similar EPA and DHA proportions (Figure 3.6). However, DHA was lower in some of the lakes in the 1-10 m depth range (i.e., VG1, VG2, VG4, VG5 and ERA5) that were shallower than the rest (max depth range 1.2 to 3.5 m). Only zooplankton from deep lakes (i.e. > 1 m) had C20:2n6 and C20:2n3 in proportions > 1% of total PUFA. The same PUFA were present in minimal proportions in zooplankton of some shallow lakes. C18 PUFA represented < 1% of total PUFA in most zooplankton, except lake LL1 where it was 2.4 % (Figure

3.6). The individual PUFA when correlated with the unicellular eukaryotic community only showed a significant correlation ($R^2 = 0.26$, $p < 0.05$) between C18:3n3 and <1m deep lakes, while the rest of the PUFA did not show significant correlations (Figure S3.6).

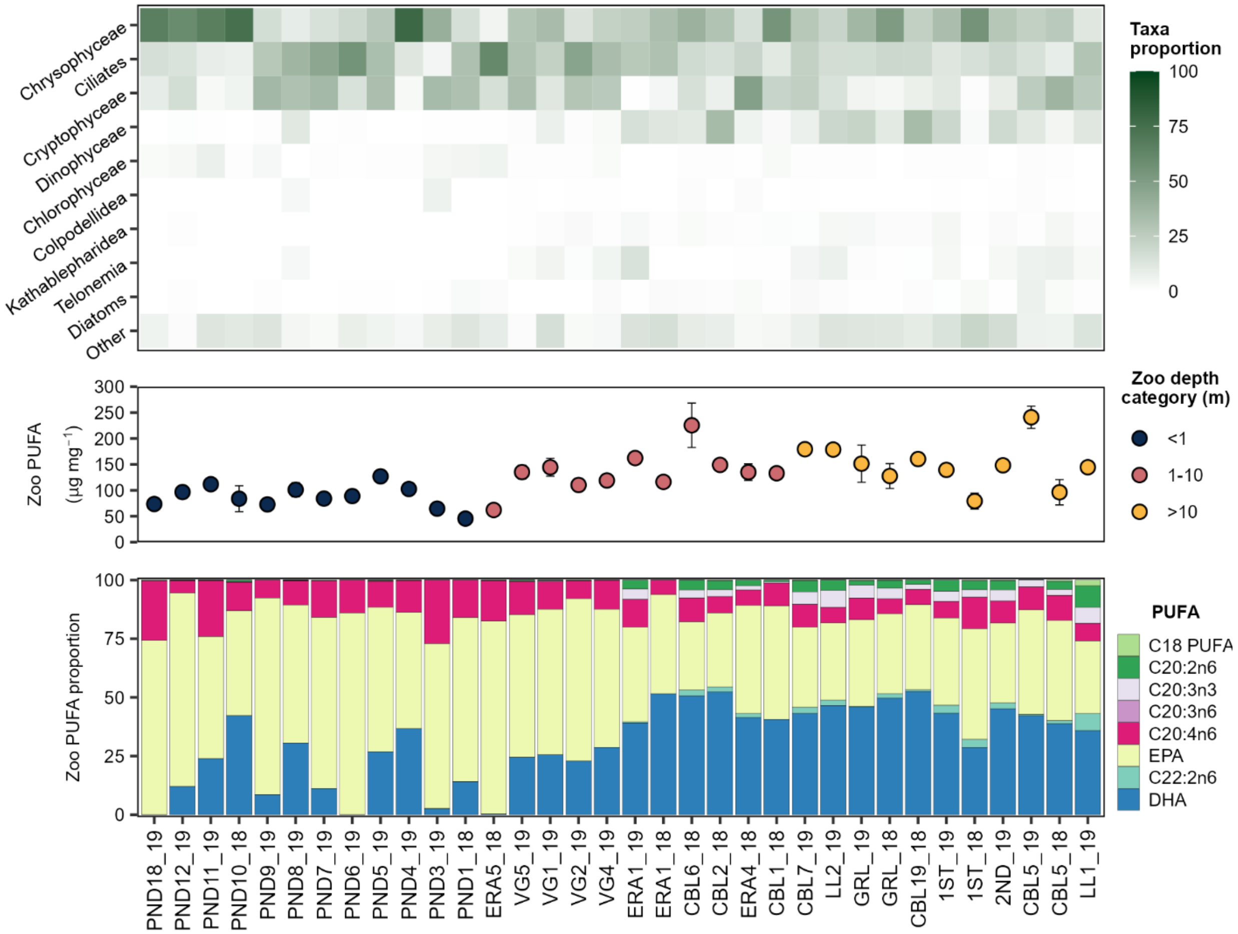

Figure 3. 6 Relative abundance of the 10 most abundant taxa in the microbial eukaryotic community (> 3 µm filter) at order level, where ciliates are grouped orders Spirotrichea, Litostomatea, Heterotrichea, CONTH 7 and CONThreeP and Diatoms are grouped orders Mediophyceae, Coscinodiscophyceae, and Bacillariophyceae, others are taxa that were present in less than 1% in 95% of the samples. Total PUFA content in zooplankton and zooplankton PUFA composition in a lake depth gradient. Lakes are organized by increasing maximum depth.

No single microbial eukaryotic taxa or combination of taxa was unequivocally "best" for explaining PUFA content in zooplankton, with eight models having AICc values within two of the "best" model and nine models in all falling within the model confidence interval set (Table 1). Consideration of models within the confidence interval set indicated that the most important microbial eukaryotic taxa driving zooplankton PUFA content were the Dinophyceae and Diatoms which were included in all the considered models had resulting Akaike variable importance weights of 1 (Table 2). While Telonemia and Chrysophycea were of moderate importance with 0.58 and 0.43, respectively. Finally, Chlorophyceae and other smaller groups had minimal influence on the PUFA content (Table 1 and S1).

Table 3. 1 Ranking of the best multiple linear regression models (based on lowest AICc) used to explain differences in PUFA content in zooplankton along the lake depth gradient. Differences (Δ_i)

#		Model	Δ_i	R^2	w_i	Σw_i
1	PUFA =	Chrysophyceae+Telonemia+Cryptophyceae+ Dinophyceae+Ciliates+Diatoms	0.00	0.59	0.17	0.17
2	PUFA =	Chrysophyceae+Telonemia+Dinophyceae-Others+Diatoms	0.68	0.56	0.12	0.29
3	PUFA =	Dinophyceae-Others+Diatoms	0.88	0.50	0.11	0.40
4	PUFA =	Telonemia+Dinophyceae-Others+Diatoms	0.90	0.53	0.11	0.51
5	PUFA =	Telonemia+Dinophyceae+Diatoms	0.91	0.50	0.11	0.62
6	PUFA =	Dinophyceae+Diatoms	1.01	0.47	0.10	0.72
7	PUFA =	Dinophyceae-Chlorophyceae+Diatoms	1.43	0.49	0.08	0.80
8	PUFA =	Chrysophyceae+Telonemia+Dinophyceae+Diatoms	1.73	0.51	0.07	0.88
9	PUFA =	Kathablepharidea+Dinophyceae+Diatoms	2.00	0.48	0.06	0.94
10	PUFA =	Chrysophyceae+Dinophyceae-Others+Diatoms	2.01	0.51	0.06	1.00

Table 3. 2 The overall importance weights (Σw_i) for each microbial eukaryotic group when used as a predictor variables in the PUFA models (described in Table S1). The most important variables for explaining variation in the dependent variable are bolded.

Variables	Σw_i
Dinophyceae	**+1.00**
Diatoms	**+1.00**
Telonemia	+0.58
Chrysophyceae	+0.43
Others	-0.40
Cryptophyceae	+0.17
Ciliates	+0.17
Chlorophyceae	-0.08
Kathablepharidea	+0.06

3.5 Discussion

We quantified contents and composition of PUFA in zooplankton in Arctic lakes and identified the main trophic pathways of these health determining compounds from pelagic and benthic primary producers to secondary consumers. We show how deeper lakes offer sources of pelagic nature, richer in PUFA for zooplankton, while shallower lakes offer a mixed diet between pelagic and benthic sources with lower content of PUFA. Our results are consistent with earlier studies that have shown the benthic diet dependence of zooplankton can be substantial in shallow lakes (Rautio & Vincent, 2006; Rautio & Vincent, 2007), but that pelagic primary production is the principal PUFA source of most zooplankton (Mariash et al., 2014). We further studied the microbial eukaryotic plankton community composition in the lakes and related it to the PUFA composition in zooplankton. We supported our working hypothesis indicating that Dinophyceae and diatoms would represent the highest quality food sources for zooplankton. However, the presence of dinoflagellates showed to be more determinant for DHA content. We further show that the microbial plankton composition was defined by lake depth, likely as a response to the chemistry of the water that varies among lakes (Ayala-Borda et al., 2024a). Consequently, the nutritional quality of food sources available for zooplankton was different from shallow headwater lakes to deep, highly connected lakes. The microbial eukaryotic taxa strongly associated to deeper hydrologically connected, more oligotrophic lakes provided better nutritional quality for zooplankton. To our knowledge, no other study has provided this level of integration between lake morphometry, microbial plankton composition and nutritional quality of zooplankton for Arctic lakes before.

3.5.1 Variability in benthic and pelagic trophic pathways among lakes

In this study we show that food source for zooplankton in lakes of the Greiner Lake watershed varied depending on the type of lakes they inhabited. Based on their $\delta^{13}C$ and $\delta^{15}N$ values, the zooplankton communities in large and deep lakes fed exclusively on phytoplankton. However, most zooplankton in the shallowest < 1 m lakes had $\delta^{13}C$ values that were intermediate between phytoplankton and benthic mat values. These results suggest that although phytoplankton made substantial contributions to zooplankton diets, benthic carbon sources supplemented the diet in shallow lakes. The variability in the stable isotope values would be consistent with the difference in the composition of the microbial eukaryotic plankton, with higher contributions of benthic resuspended algae being made to the total algal pelagic biomass in shallow lakes. The differences in feeding modes between copepods in large lakes and Cladocerans in the smaller lakes (Blackburn-Desbiens et al., 2023) would also contribute to the observed variation. In addition, copepods tend to have higher $\delta^{15}N$ values compared to Cladocerans (Kankaala et al., 2010), who use a filter-feeding strategy and are less selective with their diet (Kerfoot & Kirk, 1991). The difference in zooplankton community composition among lakes thus helps explaining the significant difference in zooplankton PUFA content between shallow lakes (<1 m) and deeper lakes (1-10 and >10 m). Further, benthic algae are a direct food source for Cladocerans in shallow Arctic lakes (Hecky & Hesslein, 1995; Rautio & Vincent, 2007), which explains the closeness of the $\delta^{13}C$ values for benthic mats and shallow lake Cladoceran dominated zooplankton communities. The higher dependence of zooplankton on benthic resources in shallow lakes is not surprising as these lakes have most with primary production and algal biomass occurring at the bottom of the lakes (Bonilla et al., 2005; Rautio et al., 2011). Additionally, the soft surface benthic mats (i.e., not attached to rocks) are accessible to shallow lake resident zooplankton as particles are easily resuspended with minor substrate perturbations or as a result of wind mixing, with winds averaging 19.1 km h^{-1} from May to September during the open water season (Environment and Climate Change Canada, 2024). Thus, the food sources in shallow < 1 m lakes, although supporting a highly productive zooplankton community (Blackburn-Desbiens et al., 2023), offer less PUFA diversity and less high-quality PUFA sources for zooplankton, compared to deeper lakes.

Other putative diet sources in our study included seston, terrestrial soils and vegetation. Seston is a mixture of suspended materials and living cells, the latter typically making up only 5-15% of the organic matter in Arctic lakes (Rautio & Vincent, 2006; Stross et al., 1980). The isotopic signature of seston most likely describes the composition of suspended particulate organic matter, particularly in the smallest and shallowest lakes prone to evapoconcentration (Ayala-Borda et al., 2024a) and wind mixing. In deeper lakes, the relative proportion of algal material likely increased, as suggested by the higher PUFA concentration of seston in these lakes. Nevertheless, although zooplankton likely fed on seston, or at least its algal component, it is often difficult to match seston stable isotope values with consumer values given that many zooplankton selectively feed on the best quality particles among seston (Keva et al., 2023; Kleppel, 1993). Thus, we suggest that the comparison of zooplankton stable isotope values with the composition of the microbial plankton and benthic mats provides more accurate information of the relative importance of these food sources.

Terrestrial soils and vegetation can enter zooplankton food chains in boreal studies, through the leaching-DOM-microbial upgrading loop (e.g., Grosbois et al., 2020), and may be a carbon sources for zooplankton in Arctic lakes following permafrost thaw and Arctic greening (Wauthy et al., 2018). In our study, zooplankton appear less likely to obtain high quality resources from the soil as it was poor in PUFA content (Figure 3.7). Although terrestrial vegetation can have high PUFA content (Figure S3.7; Grosbois et al., 2022) terrestrial particles are often too large to be effectively filtered by zooplankton and it is preferentially processed by aquatic insect shredders and decomposers before being made available for zooplankton (Graça, 2001). Further, given the location of lakes on the treeless tundra with only few shrubs, terrestrial vegetation generally was not available to support lake food webs in the lakes studied. Additionally, a previous study showed that the composition of the organic matter in all lakes of the Greiner Lake watershed was dominated by autochthonous carbon, although deep, highly connected lakes received higher terrestrial input (Ayala-Borda et al., 2024a), allochthonous inputs were low compared to other Arctic freshwater systems. Nevertheless, terrestrial vegetation is a poor source of carbon for zooplankton in laboratory experiments (Taipale et al., 2015a). Similar to conclusions regarding the limited PUFA contributions of terrestrial carbon to zooplankton Grosbois et al. (2022) noted a small contribution from terrestrial sources in their food web study of Greiner Lake.

3.5.2 Microbial eukaryotic plankton as sources of PUFA to zooplankton

The differences in the microbial eukaryotic community among the lake depth groups were attributed to the relative abundance of four major groups: Chrysophycea, ciliates, Cryptophyceae and Dinophyceae. In the shallowest lakes the community was dominated by Chrysophyceae or ciliates, whereas in the deeper 1-10 and >10 m lakes the four groups occurred in relatively even proportions. Based on amplicons, diatoms did not represent a large proportion of the microbial eukaryotic plankton community in this study. However, phytoplankton counts from the same lakes in a previous study indicate that diatoms (Bacillariophyta) are present and can represent between 1 and 73% of the algal biovolume of lakes (Ayala-Borda et al., 2021). As with other algae diatom concentrations vary with lake depth (Hazuková et al., 2021), with pelagic diatoms favored in deeper lakes. Evidence from multiple linear regression (MLR) analysis further supports the likely contribution, showing that higher PUFA contents in zooplankton were best explained by the proportions of Dinophyceae and Diatoms.

Larger lakes although having lower nutrient concentrations in the surface provided deeper areas in the lake for algae adapted to low light conditions, and thus, promoted a microbial eukaryotic community structure with higher abundances of dinoflagellates and other mixotrophs (Modenutti et al., 2004). These taxa produce PUFA and trophically upgrade DOM of all sources, thereby providing essential elements for zooplankton growth (Tang et al., 2018; Traboni et al., 2021). In our study their presence offered a higher quality PUFA source for zooplankton in the deeper >10 m lakes. Dinoflagellates show preference for oligotrophic lakes with low DOC content (Hazuková et al., 2021) and deeper zones with low photosynthetically active radiation (Modenutti et al., 2004), consistent with higher abundance in all lakes with depths >1 m. Deeper lakes also tend to have lower concentrations of DOC and DIC due to the dilution effect of larger water volumes (Ayala-Borda et al., 2024a). The microbial eukaryotic and prokaryotic communities vary as previously reported by Potvin et al. (2021), where the eukaryotic community of lakes close to Cambridge Bay were affected by water chemistry and lake size. The contrasting microbial eukaryotic community composition along the depth gradient in our study, indicated higher PUFA content was associated with more complex food webs in deeper, highly hydrologically connected lakes (Post, 2002). Primary bacterial consumers, such as Dinophyceae or other heterotrophs (e.g., Kathablepharidea, Telonemia, Litostomatea) in larger, deeper lakes, occupied a greater fraction of the community, and thus adding PUFA to zooplankton diet, similar to results found by Traboni et al. (2021). Although the PUFA content of dinoflagellates was not determined by Traboni et al. (2021), other studies indicate high DHA content in dinoflagellates that exceeds that of diatoms (Peltomaa et al., 2019). In shallow lakes, the opposite was observed, indicating a shorter planktonic food chain composed mostly of heterotrophs such as ciliates that in some cases may be too big for some zooplankton (Lu & Weisse, 2022), or heterotrophic bacteria that are more abundant in these shallow lakes (Ayala-Borda et al., 2021) and do not provide PUFA or sterols for zooplankton (Martin-Creuzburg et al., 2011).

The dominance of Dinophyceae in the microbial eukaryotic community translated into higher PUFA content, but especially high relative amounts of DHA in the total PUFA content found in deep lake zooplankton. As hypothesized, zooplankton in deeper lakes had higher PUFA content because the available pelagic planktonic food sources were not only more abundant, but also different compared to shallower lakes. The variability in DHA content in shallow <1 m lakes can be related to the zooplankton composition of these lakes. Most of the lakes that had low DHA in zooplankton were dominated by cladocerans previously reported as having low DHA content

(Makhutova et al., 2014; Persson & Vrede, 2006). Additionally, the shallow lake environment provides a mix of food sources ranging from primary producers in the water column, to soft sediments, and suspended particles. Zooplankton turn to benthic sources as food when the planktonic sources are scarce (Siehoff et al., 2009), which explains the low PUFA contents in shallow lakes. These results highlight the importance of pelagic algae as a high-quality food source for zooplankton in deep lakes and the dependence of zooplankton in shallow lakes on benthic sources.

An increasing trophic state in shallower lakes can also lead to decreasing PUFA content, acting as a driver for cyanobacterial growth (Bonilla et al., 2023), with recent evidence showing they are becoming more present in the Arctic (Ayala-Borda et al., 2021). On the contrary to other pelagic primary producers, cyanobacteria do not offer enough PUFA (Ahlgren et al., 1992; Guedes et al., 2011) or other vital lipids (e.g., sterols; Peltomaa et al., 2017) important for zooplankton growth and reproduction (Bednarska et al., 2014; Elert et al., 2003). Cladocerans are more easily affected by trophic state in high latitude lakes as observed by Chaguaceda et al. (2024), while copepods can likely regulate their PUFA content by their selective feeding strategy. Although zooplankton in this study are currently able to cover their carbon demand with benthic algae, bacteria and other particulate organic matter, as evidenced in the abundant Cladoceran communities in shallow lakes (Blackburn-Desbiens et al., 2023), their growth efficiency may be affected by the poorer PUFA microbial eukaryotic plankton community (Taipale et al., 2007). While zooplankton in deeper lakes (1-10 and >10 m) do not depend on benthic sources, a change in the composition of the phytoplanktonic community towards cyanobacteria or certain mixotrophs (Senar et al., 2021) may be detrimental for zooplankton production (e.g., Vad et al., 2021). Consequently, a switch to a poor PUFA zooplankton community could affect the somatic growth and reproduction in fish

(Taipale et al., 2022) that in oligotrophic Arctic lakes are highly dependent on PUFA rich zooplankton (Grosbois et al., 2022).

3.7 Conclusions

Our study supports the importance of the microbial eukaryotic plankton as high-quality fatty acid sources for freshwater zooplankton communities and how the availability of certain taxa as food sources, notably dinoflagellates, determines the PUFA composition of the zooplankton in Arctic lakes. Zooplankton in most shallow lakes had a mixed diet, likely associated with benthic production, and resuspended particles. Although the current microbial eukaryotic plankton community offers high quality sources of fatty acids for the zooplankton diet, ongoing climate change may alter the chemical and physical properties of the water, thus shifting the community of primary producers. Water evaporation might be critical for shallow lakes risking desiccation, while shifting food web processes in deeper lakes. As lakes between 1-10 m deep become shallower, zooplankton will be forced to shift diets towards benthic sources. Finally, increased allochthonous inputs may reduce light for benthic mats in deep lakes, promoting stratification and supporting bloom forming algae with negative effects for zooplankton. Although deep lakes may be more resilient to changes due to their higher volume, the reduction of high-quality food sources for zooplankton has the potential to limit freshwater fish populations by reducing their PUFA contents and ultimately affecting the important ecosystem services these lakes provide for northern communities. We suggest further survey studies of microbial eukaryotic plankton communities in similar lakes from polar arid landscapes are needed as they can act as critical sentinels of ecosystem health in the Arctic.

3.8 Acknowledgements

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3.9 Supplementary material

3.9.1 Supplementary figures

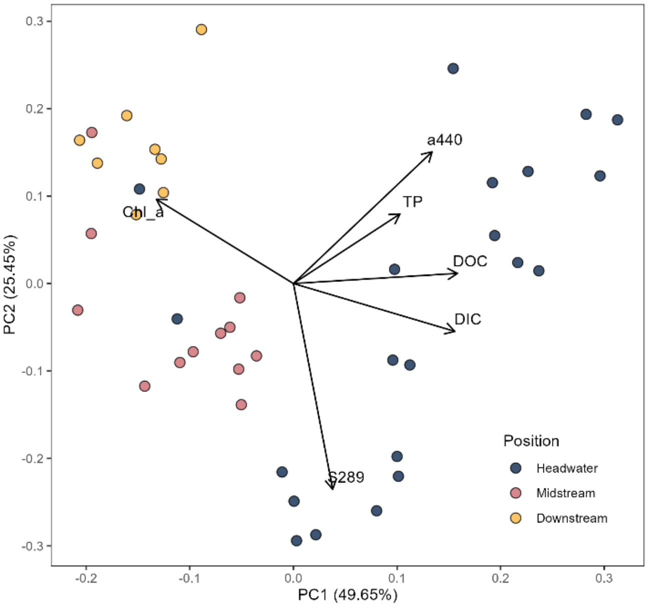

Figure S3. 1 Principal component analysis of all sites and descriptive chemical variables with lakes colored in the three hydrological connectivity gradient categories using data obtained from Ayala-Borda et al. (2024b).

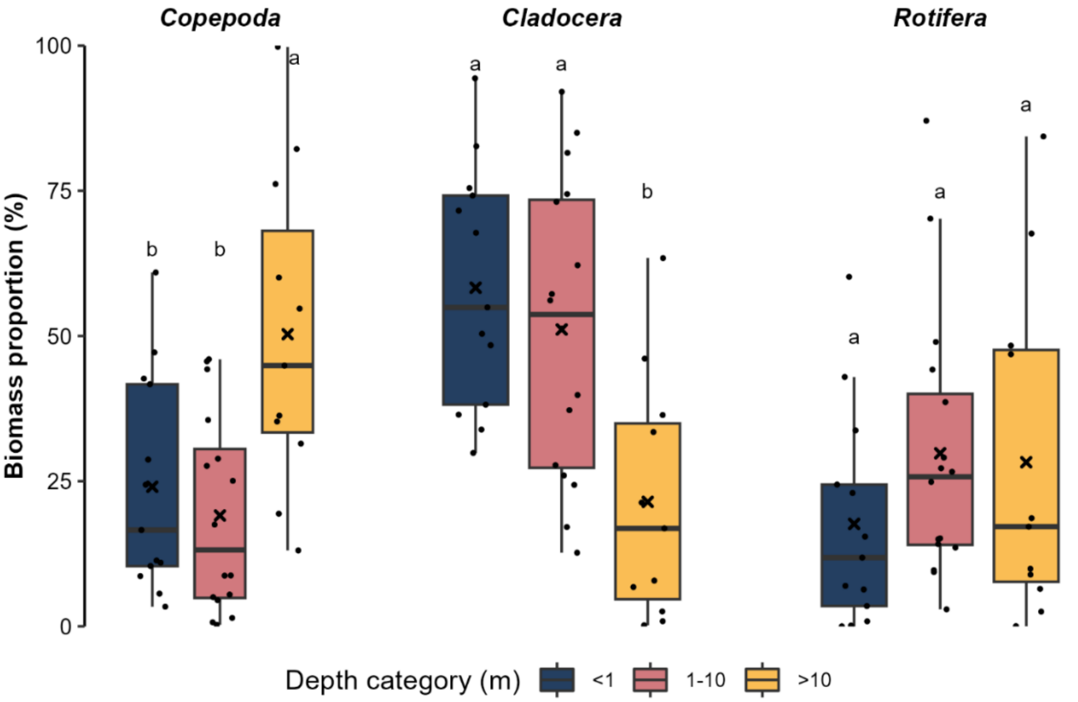

Figure S3. 2 Proportions of Copepoda, Cladocera and Rotifera taxa in the zooplankton community from studied lakes in the three depth categories as obtained from Blackburn-Desbiens et al. (2023). Different letters indicate significant differences at the α=0.05 level of significance.

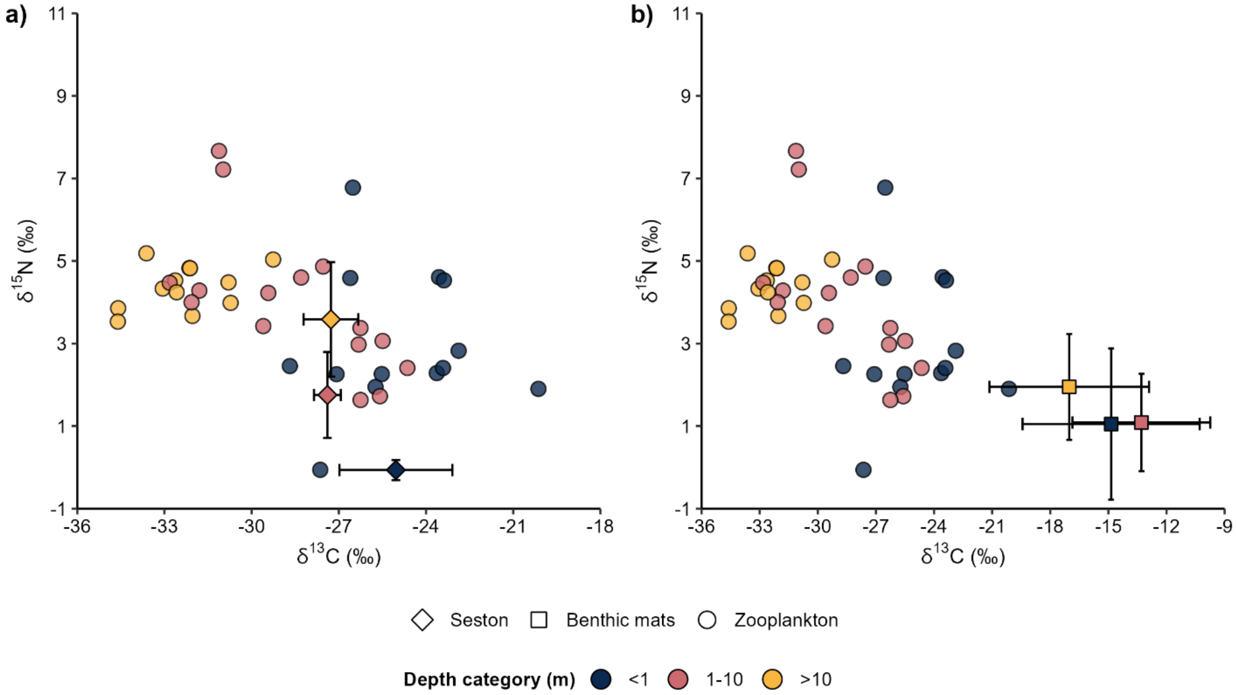

Figure S3. 3 Figure S3. Zooplankton and a) seston and b) benthic mat stable isotope values with data separated by lake depth categories.

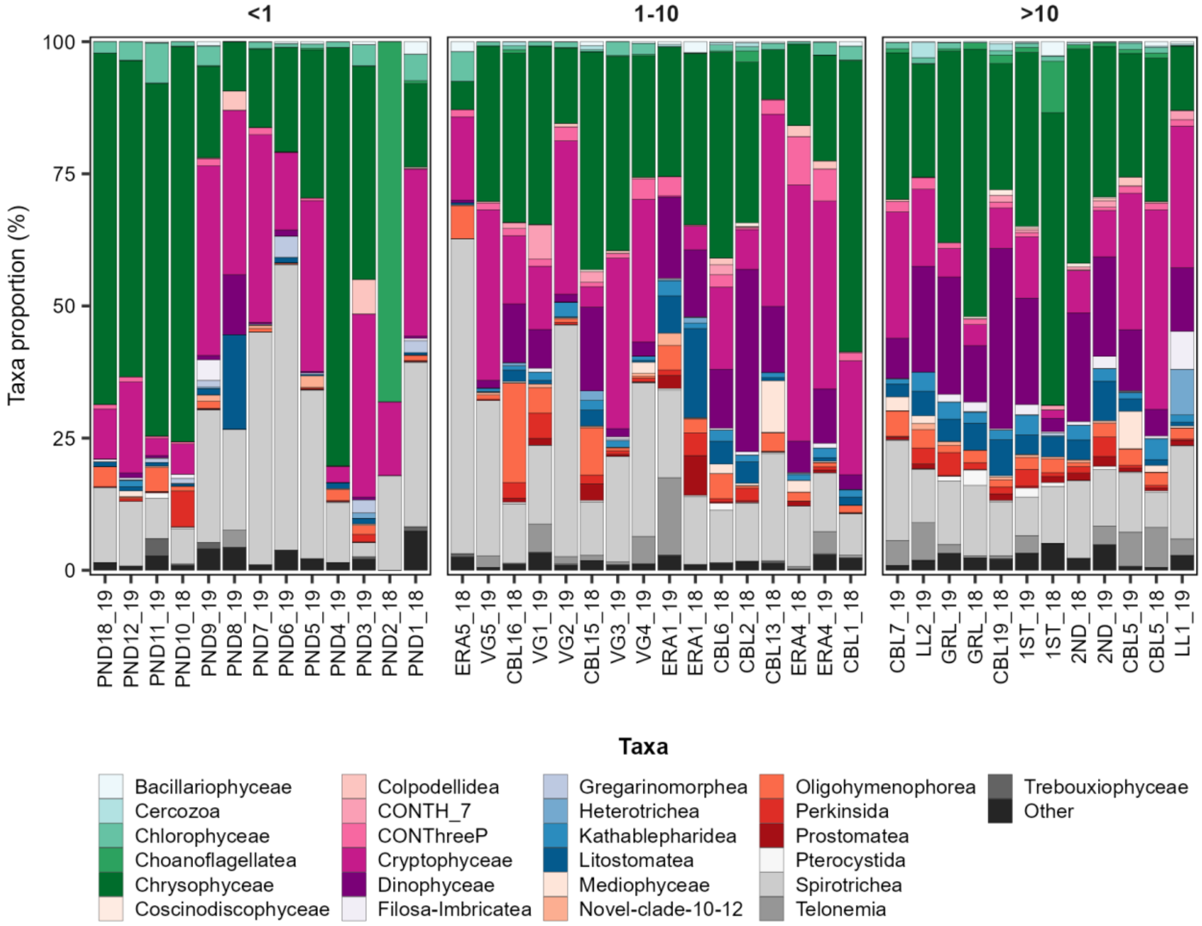

Figure S3. 4 Eukaryotic community composition (> 3 μm) of the water column in <1m, 1-10 m and >10 m deep lakes. Phyla that represented less than 5% of the total community were grouped as “Other”.

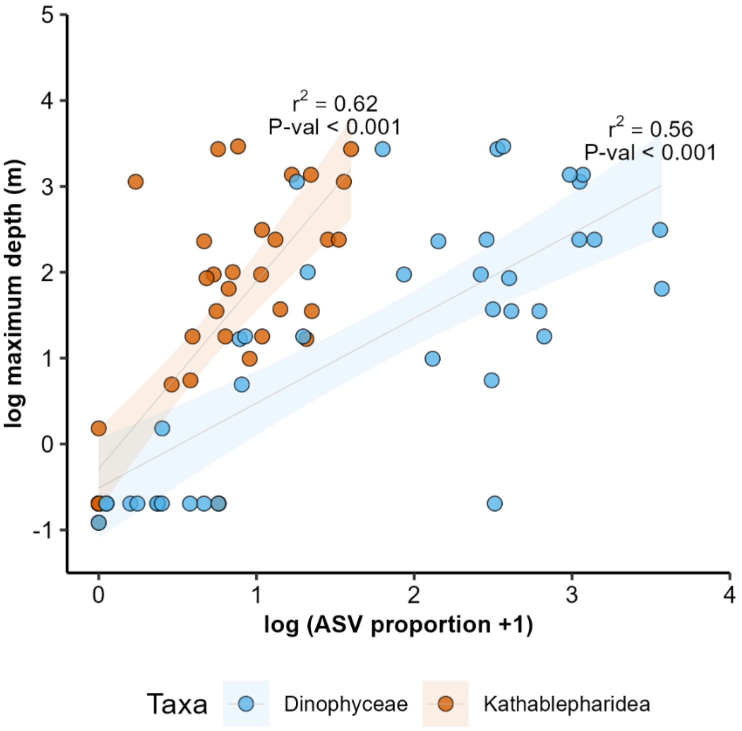

Figure S3. 5 Linear regression of Dinophyceae and Kathablepharidea with lake depth. Proportion values of each taxon and depth were log transformed.

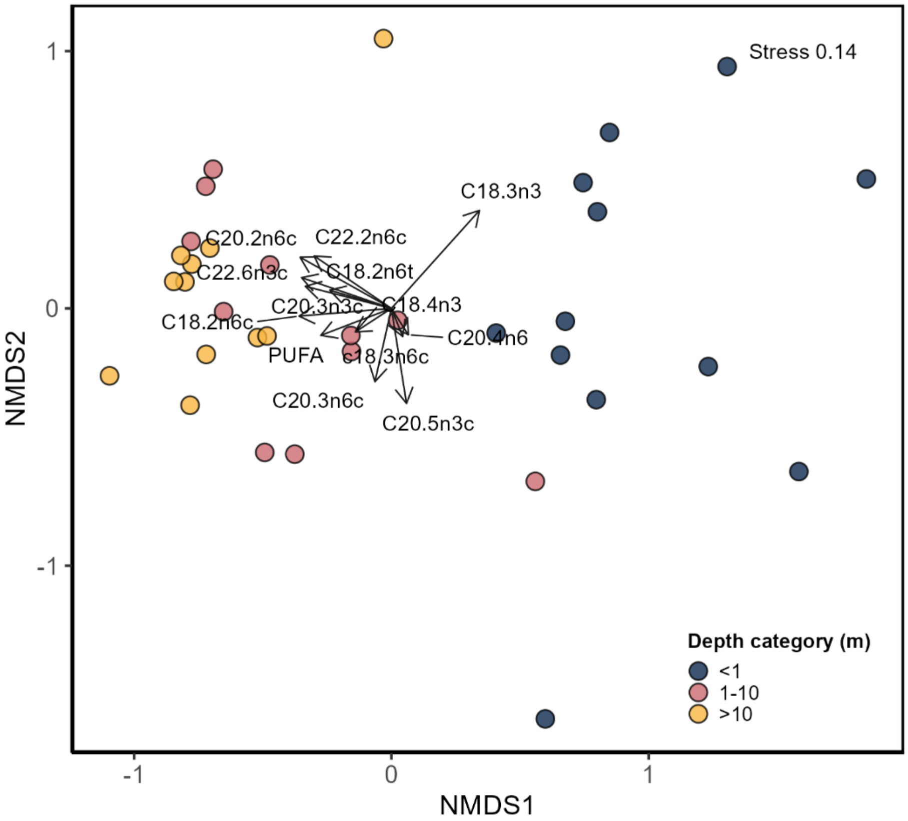

Figure S3. 6 Non-metric multidimensional scaling of unicellular eukaryotes (>3 µm) with vectors of individual zooplankton PUFA and total PUFA in the three lake depth categories.

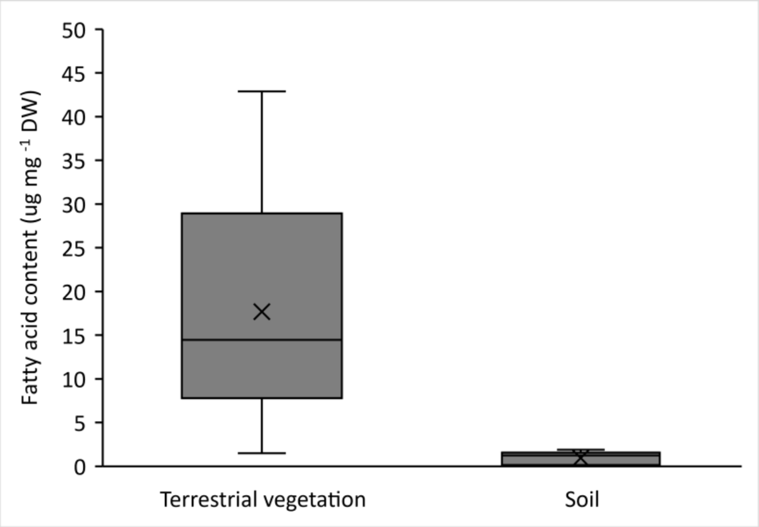

Figure S3. 7 Total PUFA content in samples of terrestrial vegetation and soil from the near shore area.

GENERAL CONCLUSIONS

The state of the Arctic biome is of general concern due to the fast changes occurring in both terrestrial and aquatic ecosystems that will inevitably impact the rest of the planet through the mobilization of carbon and the release of large amounts of stored carbon. Arctic landscapes can show great heterogeneity, varying in elevation, precipitation, soil type, and permafrost composition. These components and the way they interact with aquatic environments can result in variable responses to climate change depending on how they combine. Most studies in the Arctic are carried out in regions rich in organic soil and with increasing permafrost degradation where lakes are strongly affected by terrestrial inputs with concomitant effects on trophic state, lake metabolism and food web structure. However, Arctic freshwater ecosystems in dissimilar regions of the Arctic do not always show the same responses to increasing temperatures and other associated alterations in the environment.

This doctoral project gathered information of an Arctic watershed, describing the state of the watershed represented by a set of 35 lakes, but also showing the large physical, chemical, and biological variability within one single watershed. One of the significant contributions of this research is the representation of a dissimilar region of the Arctic, providing connectivity, limnologic, metabolic and diversity information in a region with low precipitation, a small organic layer in the soil, no apparent signs of permafrost degradation, and predominantly low relief. A study of this size and the combination of the studied variables are rare in limnology literature overall and even more so within the Arctic context.

The results of this doctoral work indicate that different aspects of hydrological connectivity had an influence on the lakes in the Greiner Lake watershed at various levels. In the first chapter this was evidenced in the trophic state of lakes, as most large and highly connected lakes were oligotrophic or ultraoligotrophic, while some smaller, disconnected, and shallower lakes were mesotrophic. However, the most surprising result was lake ERA5, which was eutrophic based on its TP content and the phytoplankton was dominated by cyanobacteria, with no apparent influence of human activity nearby. Lake ERA5 was compared to existing Arctic data, revealing that eutrophic lakes are present in the Arctic but are often overlooked. The published results of this chapter may have rung an alarm and opened a discussion on the process of eutrophication of lakes in the Arctic with increasing nutrient inputs from various sources.

In the second chapter, the metabolic state of lakes in the watershed was determined using water and oxygen isotopes that revealed that most lakes were net autotrophic or in metabolic equilibrium. The results were further supported by results of CO_2 in the water indicating metabolic equilibrium or net autotrophy. Hydrological connectivity as position in the watershed (i.e., headwater, midstream or downstream) and lake size were determinant factors for the chemical composition in the water, also affecting the amount of light penetrating to the bottom of the lake. Additionally, headwater lakes with small volumes of water were more affected by evaporation, contributing to determining the concentration of carbon and nutrients in the water. Consequently, high values of GPP in headwater lakes were the result of higher internal nutrient and carbon cycling and high light availability, while larger midstream and downstream lakes were close to metabolic equilibrium. The results shown in this chapter emphasize the importance of shallow headwater lakes as sites of net organic matter production under the present climatic conditions. However, the same shallow lakes are likely more vulnerable to increasing temperatures that may lead to a shift toward a higher trophic state, eventually becoming sites of net carbon mineralization or even facing complete desiccation.

In the third chapter, the transfer of carbon at the base of the food web was assessed with a combination of isotopic, fatty acid and molecular techniques not often used in the study of food webs. The results showed that, as expected, the composition and behavior of the planktonic communities varied with lake depth, which was highly correlated with the degree of hydrological connectivity of the lakes. Even though the major food source for zooplankton were planktonic microbial eukaryotes, zooplankton in shallow lakes also consumed benthic materials and had lower content of PUFA, compared to zooplankton rich in PUFA in deeper lakes. Further, the differences in the phytoplankton and zooplankton structure, attributed to lake depth and water chemistry, had an important effect on the PUFA composition of the zooplankton. Seston as well as zooplankton in deeper lakes (i.e., 1-10 and >10 m) were richer in DHA compared to shallow lakes (i.e., <1 m) as there seemed to be additional steps in the food web, with mixotrophs and heterotrophs concentrating and upgrading fatty acids for zooplankton consumption. Differences in zooplankton PUFA content were also attributed to the zooplankton composition, with more copepods in deeper lakes and more cladocerans in shallow lakes. Although the current state of lakes offers high-quality food sources for zooplankton and higher levels of the food web, changes in trophic state and light availability may influence the composition of the microbial eukaryotic plankton. Increasing temperatures and high evaporation rates in this region may put at risk shallow lakes, but also increase nutrient content in medium size lakes, changing the planktonic community from high to low PUFA sources for zooplankton. Ultimately, affecting food sources for fish that are highly dependent on zooplankton as part of their diet in the studied lakes.

The insights of this study highlight the importance of studying lakes in conjunction with their watersheds. This approach allows the understanding of the nature of components within the lake, and also how the watershed behaves, providing information about changes occurring in the landscape. The results presented in the three core chapters of this doctoral project showed the influence of hydrological connectivity on various aspects of lakes in the Greiner Lake watershed. The force of hydrological connectivity in combination with lake morphometry on the chemical composition of the water and its concomitant effect on various other biological components of the lakes highlights the importance of understanding the interactions between lakes and their surroundings. This particularity helped elucidate the present state of lakes, but more importantly to learn what components of the watershed are more vulnerable to ongoing climate change. In this region of the Arctic that experiences high evaporation rates, small shallow lakes that are the most abundant type of waterbodies are especially exposed to eutrophication and desiccation. In the long term, the reduction of shallow lakes would be translated into the loss of the most autotrophic sites with the highest potential to act as CO_2 sinks. While medium sized lakes might become shallower and possibly NEP will increase at first, along with trophic state, changing the phytoplankton community and reducing the sources of high-quality fatty acids for zooplankton. However, high production rates may eventually lead to a much lower NEP. Large, deep lakes may be more resilient due to the difference in volume, but the cascading effect in the food web due to the alteration of basal components and production rates can have a cost in the available food sources for zooplankton and fish. Although the future scenario is still uncertain, the fast pace at which the Arctic is being affected makes the study of Arctic ecosystems and their response to climate change an urgent matter. The faster those changes are understood, the sooner future management and adaptation plans for northern communities can be elaborated.

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