Phytoplankton communities as indicators of environmental change and nutrient deposition in the Canadian Rockies

by

Jenna Leanne Cook

A thesis submitted in partial fulfillment of the requirements for the degree of

Master of Science

in

Ecology

Department of Biological Sciences

University of Alberta

Abstract

Remote mountain water bodies integrate the impacts of regional factors (e.g. climate change, atmospheric pollutants) well because of the relative absence of confounding local perturbations (e.g. human land-use). Climatic factors can alter the abiotic environments within mountain lakes through changes in precipitation and temperature while atmospheric nutrient deposition potentially fertilizes their primary production. Therefore, changes in alpine phytoplankton communities may be among the first indicators of the cumulative impact of modern global change on mountain lake and pond ecosystems, particularly as recent rates of warming are positively correlated with elevation. I investigated the potential sensitivities of 29 alpine lake and pond ecosystems along the Eastern Front range of the Canadian Rockies to increased deposition of nitrogen (N) and phosphorus (P) were investigated based on their water chemistry (i.e. dissolved inorganic N (DIN): total P (TP) mass ratios) and phytoplankton responses to *in vitro* nutrient amendment bioassays previously conducted in 2008. Previous evidence of low DIN:TP mass ratios and experimental N amendments stimulating algal communities in shallower alpine sites motivated my hypothesis that nutrient limitation of phytoplankton shifts from being P- to N-driven with decreasing water depth from lakes to ponds. Although inferred and experimental lines of evidence of nutrient limitation agreed in 55% of all cases, there were some discrepancies involving co-limitation. Contrary to my hypothesis of ponds being N-limited, I found little evidence of N-limitation from bioassays of phytoplankton for sites shallower than 5 m in depth. Overall, most phytoplankton communities exhibited responses to nutrient amendments indicating that they were P- or NP- co-limited. Chromophytes and chlorophytes drove the greater responsiveness of whole phytoplankton communities to P relative to N.

Next, I investigated the inferred sensitivity of mountain phytoplankton to climatic factors and tested whether the nature of nutrient limitation had changed in the study area over the past 10 years as a result of nutrient deposition. Water samples were collected during the ice-free season of 2017 and 2018 from a total of 82 mountain lakes within the National Parks of the Canadian Rockies, and a subset of 14 alpine lakes chosen for nutrient enrichment bioassays, following the same protocol as the 2008 bioassays. Linear regression analysis was performed to determine significant environmental predictors of net algal production and redundancy analysis was used to determine the best set of explanatory variables of taxonomic variance in phytoplankton communities across the surveyed lakes. TP was identified as both the only significant predictor of chlorophyll-inferred phytoplankton biomass across the 82 surveyed lakes, and the key nutrient stimulating phytoplankton production in the bioassays. The bioassay results also revealed a strong synergistic response to the combined NP nutrient amendments. Results also revealed local features that mediate the influence of climate change to be the most important correlates of phytoplankton community composition, namely dissolved organic carbon and light availability along with proportion of carbonate sedimentary bedrock and bare catchment. Taken together, these findings highlight the sensitivity of phytoplankton communities in the Canadian Rockies to the indirect impacts of global warming, including the increased incidence of wildfires that fuel P deposition. The synergistic response to N and P also emphasizes a need for further research into potential fertilizing effects of combined anthropogenic N emissions and P deposition on lake ecosystems at high elevations.

Preface

A portion of this thesis reflects a manuscript prepared in collaboration with fellow researchers. A version of Chapter 2 has been published as: Cook J, Stuparyk BR, Johnsen MA, Vinebrooke RD (2020) Concordance of chemically inferred and assayed nutrient limitation of phytoplankton along a depth gradient of alpine lakes in the Canadian Rockies. Aquat Sci 82:17 doi.org/10.1007/s00027-019-0683-7. I analyzed the data and composed the manuscript. Rolf Vinebrooke conceived of the idea for the study and contributed to the study design and manuscript revisions. Blake Stuparyk and Mitchell Johnsen provided feedback on data analysis and contributed to manuscript revisions.

Acknowledgements

I would first like to thank my supervisor, Rolf Vinebrooke, for his continued support, assistance and expertise. It was in his introductory limnology course that I first became interested in this field and I feel very fortunate that I have had the opportunity to be a part of his lab. I also recognize Toby Spribille for his helpful contributions serving on my supervisory committee.

I would also like to thank all the amazing people and friends that I had the pleasure of working with in the field and lab including Blake Stuparyk, Mitchell Johnsen, Katie Keenan, Charlotte Dawe, Tom Brown and Caleb Sinn. I had the best summer cramming into the cabin after long days spent out sampling in the mountains. I am so grateful for the teamwork and dedication from everybody to sample so many lakes. A special thank you to Blake, Mitchell and Caleb who helped carry water out of the alpine sites for the bioassays. It was a test of our physical and mental strength, but I think we came out stronger for it. I would also like to thank Mark Graham for the assistance along the way, including encouragement when I first started my degree. I would also like to acknowledge Conrad Murphy and Patrick Thompson who did the field work, bioassay set-up and HPLC analysis for Chapter 2, without their work the analysis would not have been possible. A thank you as well to Parks Canada for allowing us to conduct research within the national mountain parks of Canada.

On a personal note I would like to thank my parents and siblings for their encouragement, support and confidence in me. Not only in pursuing this degree, but in all aspects of my life I would not be where I am today without my wonderful family. Lastly, a special thank you to Jordan Mannix, for his constant love and encouragement, I am incredibly grateful for every assuring conversation, of which there were many.

This work was supported by an Alberta Conservation Association Grant in Biodiversity awarded to Jenna Cook and grants from the Alberta Ingenuity Center for Water Research and the Natural

Sciences and Engineering Research Council of Canada awarded to Rolf Vinebrooke, a Queen Elizabeth II Scholarship, Graduate Teaching Assistant Scholarships, and the Department of Biological Sciences Dissertation Award awarded by the University of Alberta.

Table of Contents

List of Tables

List of Figures

Chapter 1 : Introduction

Background and Rationale

Phytoplankton as Indicators of Change

Lake ecosystems integrate the effects of local and regional factors across their entire catchments and airsheds and have been identified as sentinels of environmental change (Williamson et al. 2008). Phytoplankton consists of relatively small photoautotrophic eukaryotes and cyanobacteria with short life spans, fast reproduction rates, and wide dispersal potential, which results in them being very responsive to environmental changes (Schindler 1987). These algae and cyanobacteria integrate chemical changes occurring terrestrially and atmospherically, responding to a wide range of pollutants and thermal variations, leading to them being labelled as bioindicators (McCormick and Cairns 1994; Williamson et al. 2008; Adrian et al. 2009; Parmar et al. 2016). For example, Schindler (1987) summarized findings from several whole-lake experiments conducted at the Experimental Lakes Area and emphasized that shifts in boreal phytoplankton communities were among the most sensitive indicators of the early stages of stress to lake ecosystems. They can better integrate the biological effects of environmental changes over time, providing meaningful ecological information that cannot be obtained through routine intermittent environmental monitoring of water quality of surface waters (Reynolds 2006; Adrian et al. 2009).

Phytoplankton in mountain lakes and ponds can serve as warning systems because climate-driven impacts are frequently accelerated at higher elevations, and the relatively pristine nature of many remote mountain lakes make them especially sensitive to extreme or novel anthropogenic perturbations, or “stressors” (Catalan et al. 2013). Being relatively removed in many cases from local anthropogenic disturbance, mountain lakes can better represent average global changes, filtering some noise caused by human perturbations (Adrian et al. 2009; Catalan et al. 2013). Several variables change predictably with elevational gradients including temperature, ultraviolet (UV) radiation and UV-attenuating dissolved organic carbon (DOC) concentration. This knowledge allows a space-for-time substitution for lakes studied within the same geographic area and the possibility to test the response to environmental change (Moser et al. 2019). Mountain lakes have become reference points, used to evaluate current and future effects of anthropogenic pollution (Catalan et al. 2013).

Importance of Mountain Lakes as Headwaters

The vulnerability of mountain lakes has important implications beyond their own water quality because they provide water to downstream, lowland regions (Viviroli et al. 2007). It has been estimated that half of the global population is dependent on water originating from mountains for power and water supplies (Woodwell 2004). Some mountain lakes are already experiencing decreased water quality (Thies et al. 2007; Bajard et al. 2018). Thus, mountain research involving predictive effects of climate change will not only serve as a warning, but also have important implications for water management.

Atmospheric Deposition of Nutrients to Mountain Lakes

The chemically dilute and unproductive, or “oligotrophic”, nature of alpine lakes and ponds allows them to be early indicators of deposition of external nutrients (Murphy et al. 2010) and even small changes in nutrient concentrations can have relatively large impacts (Sickman et al. 2003; Baron et al. 2011). Nitrogen (N) and phosphorus (P) are the two nutrients that often limit the growth of freshwater primary producers (Reynolds 2006). Human activity has increased the reactive nitrogen globally, through agricultural practices and combustion of fossil fuels (Vitousek et al. 1997). N is primarily deposited as wet deposition, with alpine sites often receiving higher N input through greater precipitation than lower elevations (Moser et al. 2019). P is deposited as dry deposition, released through biomass burning such as wildfires and contained in aeolian dust, which can be transported extended distances (Mahowald et al. 2008; Zhang et al. 2018).

Nutrient input to alpine lakes is a current topic of interest because it can stimulate primary productivity or impact the limiting nutrient of the system. The limiting nutrient is often predicted by the in-lake dissolved inorganic nitrogen (DIN): total phosphorus (TP) mass ratio, which represents the biologically available N and P to phytoplankton (Morris and Lewis 1988; Bergström 2010). Moreover, lake nitrate concentrations are strongly correlated with the amount of N deposition (Bergström and Jansson 2006; Elser et al. 2009). Thus, the deposition of nutrients can alter the limiting nutrient. However, some previous studies have found the DIN:TP mass ratio alone was not always accurate in predicting the limitation type, particularly for co-limitation by N and P (Slemmons and Saros 2012; Symons et al. 2012; Daggett et al. 2015; Williams et al. 2016).

Studies within the United States have found mountain lakes to be naturally N-limited, with increased N deposition resulting in a switch to P-limitation (Bergstöm and Jansson 2006; Elser et al. 2009). The United States have implemented long-term atmospheric monitoring of N deposition, the National Atmospheric Deposition Program (NADP), with 186 sites across the country to collect wet N deposition records (Baron et al. 2011). Results from the NADP have revealed elevated N deposition in the Sierra Nevada and US Rocky Mountains, with estimates of critical load revealing high-elevation sites are most vulnerable to the impacts of elevated N deposition, several of which have already been reached (Baron et al. 2011; Nanus et al. 2012). However, P deposition is frequently overlooked, though changes in alpine algal assemblages have been linked to P deposition (Brahney et al. 2014; Brahney et al. 2015).

Atmospheric deposition of nutrients over the Canadian Rockies remains largely unknown relative to other parts of the industrialized world. However, lakes in the Canadian Rockies are generally situated in less developed areas than those in Norway, Sweden and the Colorado Sierra Nevada where high rates of N deposition have been recorded (Elser et al. 2009). There is a likelihood that N and P deposition rates will increase, due to growing populations, continued use of fossil fuels and greater agricultural pressure, and a predicted increase in frequency and extent of wildfires in western Canada due to climate change (Wang et al. 2017). This provides an opportunity to assess the potential sensitivity of lakes to nutrient deposition over the Canadian Rockies, a region that is assumed to be relatively unimpacted thus far by atmospheric deposition of N and P. Here, previous research on alpine ponds showed that their low DIN:TP mass ratios (McMaster and Schindler 2005; Murphy et al. 2010) are indicative of the algal communities being highly responsive to experimental additions of N (Vinebrooke et al. 2014), making these ecosystems potentially very sensitive to future increases in N deposition.

Anticipated Changes Associated with Warming

Characterized by colder temperatures, long periods of ice and snow cover, hydrology dominated by snow and glacier melt and frequently chemically dilute, mountain lakes are especially vulnerable to climate-driven events (Catalan et al. 2013). Alpine sites are warming at a faster rate due to elevation dependent warming (Wang et al. 2014; Pepin et al. 2015; Palazzi et al. 2019). Warmer air temperatures have several effects on lakes including warmer surface temperatures, longer ice-free seasons, earlier snowmelt, changes in snowpack and continued melting of glaciers (Thompson et al. 2005; Clow 2010; Fountain et al. 2012; Huss et al. 2017). Preston et al. (2016) presented long-term ice-off data for seven Colorado alpine lakes revealing that ice-off dates were seven days earlier over the 33-year span of the study, and the length of the ice-free season is projected to lengthen further (Roberts et al. 2017). A longer ice-free season could result in increases in primary productivity (Vinebrooke et al. 2010). The timing of snowmelt is shifting as well. Clow (2010) found that over a 29-year span peak snowmelt shifted 2-3 weeks earlier in the Colorado Rockies. Nutrients often accumulate in the snowpack, and lakes receive a nutrient pulse when snowmelt begins after winter (Fountain et al. 2012). The timing of snowmelt can also affect other in-lake processes, affecting lake hydrology and phytoplankton biomass (Huss et al. 2017; Sadro et al. 2018). Responses associated with climate change could also result in the advancement of treelines, which could contribute to brownification of nearby lakes through increased terrestrial loading of coloured allochthonous DOC (Vinebrooke and Leavitt 1998).

Glaciers continue to recede, currently at accelerated rates (Fountain et al. 2012) with predictions of a 90% loss by 2100 in the Canadian Rockies (Clarke et al. 2015). Glaciers can be a source of pollutants such as organochlorine (Blais et al. 2001), or nutrients like nitrogen and DOC when lakes are glacially-fed (Slemmons et al. 2013; Li et al. 2018; Colombo et al. 2019). In studies in the US Rocky Mountains, nitrate concentrations were 40 times greater in glacially fed lakes and experienced greater primary productivity compared to snowpack-fed lakes (Slemmons and Saros 2012; Slemmons et al. 2017). The high N content in the meltwater was attributed to previously deposited and stored nutrients (Slemmons and Saros 2012). However, the nitrate content can vary regionally due to differences in N deposition, geology or climate. A study in the North Cascades found no positive relationship between glacier area and lake nitrate, and no differences in phytoplankton biomass between glacially and non-glacially fed lakes (Williams et al. 2016).

The phytoplankton response to glacial melting can also result from changes in turbidity. Glacier meltwater contains a high concentration of suspended minerals, termed glacial flour, which increases lake turbidity thereby reducing light availability (Sommaruga 2015). Vinebrooke et al. (2010) found in a paleolimnological study in the Canadian Rockies that when an alpine lake was glacially fed, primary productivity was reduced owing to the colder temperatures and reduced light. Primary productivity increased following the ablation of the glacier (Vinebrooke et al. 2010). Therefore, the effects of melting glaciers are complex, with varying factors involving geology, soil and vegetation cover, glacial flour content and historic nutrient deposition.

Value of Pond Studies

Much of our understanding of the effects of climate change have come from deeper waterbodies, however smaller and shallower waterbodies (< 5 m; hereafter referred to as ‘ponds’), may respond differently to the effects of climate change. The shallow nature allows UV light to penetrate to the bottom sediment which could favour more UV tolerant taxa. Additionally, they are polymictic and strong mountain winds can result in complete mixing, potentially releasing stored nutrients from the sediment (Orihel et al. 2015). Ponds also respond readily to changes in temperature and precipitation because the lower volume does not as effectively dilute deposited nutrients compared to large lakes (McMaster 2003). The importance of pond studies is also reinforced by their pervasiveness, as they make up more area globally than lakes (Downing 2010), and in Banff National Park alone there are over 3000 alpine ponds (McMaster and Schindler 2005).

Conclusion

Mountain lakes are sentinels of change, and phytoplankton respond rapidly to even subtle changes. Conducting a large-scale survey of mountain lakes offers an opportunity to investigate the potential of phytoplankton communities to serve as bioindicators of ecological impacts of various local and regional environmental changes on their phytoplankton. There are several predicted changes associated with climate change for mountain lake ecosystems, including enhanced external deposition of nutrients, alterations on snowmelt timing, changes in DOC concentration, increased glacier melting, and longer ice-free seasons with higher lake temperatures. Several factors may have negative effects, leading to enhanced algal growth or changes to phytoplankton communities, potentially deteriorating headwaters which is particularly concerning given the importance of water originating in the mountains. The question also remains whether deeper water bodies will respond differently than shallow ponds to changes in climate and anthropogenic effects such as enhanced nutrient deposition.

Main Research Objectives:

1) Determine if alpine lakes versus ponds differ in their sensitivity to N or P deposition (Chapter 2).
2) Investigate how well chemically inferred and experimental nutrient enrichment experiments agree in their conclusions of nutrient limitation (Chapter 2).
3) Identify the best set of measured environmental variables explaining the variation in phytoplankton abundance and community composition across an elevational gradient which consists of 82 mountain lakes and ponds in the Canadian Rockies (Chapter 3).
4) Determine if the limiting nutrient within alpine lakes and ponds in the Eastern Front range of the Canadian Rockies in 2018 has shifted after ten years of nutrient deposition (Chapter 3).

To achieve the first two objectives, 29 alpine lakes and ponds were previously surveyed in 2008 for water chemistry and phytoplankton communities, which were each assayed *in vitro* for nutrient limitation using crossed factorial (N × P) experiments. After a 12-day incubation in the growth chamber, the concentrated pigments from each vial were extracted using high-performance liquid chromatography (HPLC) for pigment analysis. I then analyzed the HPLC chromatograms and used one-way analysis of variance (ANOVA) to determine the limitation type for each site. These results were compared to inferred limitation types using the DIN:TP mass ratios which categorize N-, co- or P-limitation dependent on known thresholds. To determine if lakes and ponds differ in their sensitivity to N versus P a linear regression analysis of depth and DIN:TP mass ratio was performed.

To achieve the third objective, we surveyed 82 mountain lakes within 5 national parks in the Canadian Rockies in 2017 and 2018. At each site, an integrated water sample was taken for later chemical analysis of key nutrients, 1000 mL was filtered to concentrate phytoplankton for later HPLC analysis, and physical factors were measured *in situ* from the deepest point of each lake. With the catchment, chemical and physical data from each lake and phytoplankton community data from HPLC analysis, a redundancy analysis (RDA) and ordination were used to determine the key drivers of the phytoplankton communities.

To achieve the fourth objective, N × P enrichment bioassays were performed from a subset of 14 alpine lakes from the 82-lake survey. Following the same methodology as in 2008, the form of nutrient limitation was determined, and the overall limiting nutrient for the Eastern Front ranges of the Candian Rockies was compared to the results from Chapter 2.

Literature Cited

Adrian R, O'Reilly CM, Zagarese H, Baines SB, Hessen DO, Keller W, Livingstone DM, Sommaruga R, Straile D, Van Donk E, Weyhenmeyer GA, Winder M (2009) Lakes as sentinels of climate change. Limnol Oceanogr 54:2283-2297

Bajard M, Etienne D, Qiunsac S, Dambrine E, Sabatier P, Frossard V, Gaillard J, Develle A-L, Poulenard J, Arnaud F, Dorioz J-M (2018) Legacy of early anthropogenic effects on recent lake eutrophication (Lake Bénit, northern French Alps). Anthropocene 24:72-87

Baron JS, Driscoll CT, Stoddard JL, Richer EE (2011) Empirical critical loads of atmospheric nitrogen deposition for nutrient enrichment and acidification of sensitive US lakes. BioScience 61:602-613

Bergström A-K (2010) The use of TN:TP and DIN:TP ratios as indicators for phytoplankton nutrient limitation in oligotrophic lakes affected by N deposition. Aquat Sci 72:277-281

Bergström A-K, Jansson M (2006) Atmospheric nitrogen deposition has caused nitrogen enrichment and eutrophication of lakes in the northern hemisphere. Global Change Biol 12:635-643

Blais JM, Schindler DW, Muir DCG, Sharp M, Donald D, Lafrieniere M, Braekvelt E, Strachan WMJ (2001) Melting glaciers: A major source of persistent organochlorines to subalpine Bow Lake in Banff National Park, Canada. Ambio 30:410-415

Brahney J, Ballentyne AP, Kociolek P, Spaulding S, Otu M, Porwoll T, Neff JC (2014) Dust mediated transfer of phosphorus to alpine lake ecosystems of the Wind River Range, Wyoming, USA. Biogeochemistry 120:259-278

Brahney J, Mahowald N, Ward DS, Ballantyne AP, Neff JC (2015) Is atmospheric phosphorus pollution altering global alpine lake stoichiometry? Global Biogeochem Cycles 29:1369-1383

Catalan J, Bartrons M, Camarero L, Grimalt JO (2013) Mountain waters as witnesses of global pollution. In: Pechan P, de Vries GE (eds) Living with water: Targeting quality in a dynamic world. Springer, New York, pp 31-67

Clarke GKC, Jarosch AH, Anslow FS, Radic V, Menounos B (2015) Projected deglaciation of western Canada in the twenty-first century. Nature Geoscience 8:372-377

Clow DW (2010) Changes in the timing of snowmelt and streamflow in Colorado: A response to recent warming. J Clim 23:2293-2306

Colombo N, Bocchiola D, Martin M, Confortola G, Salerno F, Godone D, D'Amico ME, Freppaz M (2019) High export of nitrogen and dissolved organic carbon from an alpine glacier (Indren Glaciers, NW Italian Alps). Aquat Sci 81:74

Daggett CT, Saros JE, Lafrancois BM, Simon KS, Amirbahman A (2015) Effects of increased concentrations of inorganic nitrogen and dissolved organic matter on phytoplankton in boreal lakes with differing nutrient limitations patterns. Aquat Sci 77:511-521

Downing JA (2010) Emerging global role of small lakes and ponds: little things mean a lot. Limnetica 29:9-24

Elser JJ, Anderson T, Baron JS, Bergström A-K, Jansson M, Kyle M, Nydick KR, Steger L, Hessen DO (2009) Shifts in lake N:P stoichiometry and nutrient limitation driven by atmospheric nitrogen deposition. Science 326:835-837

Fountain AG, Campbell JL, Schuur EAG, Stammerjohn SE, Williams MW, Ducklow HW (2012) The disappearing cryosphere: Impacts and ecosystem responses to rapid cryosphere loss. BioScience 62:405-415

Huss M, Bookhagen B, Huggel C, Jacobsen D, Bradley RS, Clague JJ, Vuille M, Buytaert W, Cayan DR, Greenwood G, Mark BG, Miler AM, Weingartner R, Winder M (2017) Toward mountains without permanent snow and ice. Earth's Future 5:418-435

Li X, Ding Y, Xu J, He X, Han T, Kang S, Wu Q, Mika S, Yu Z, Li Q (2018) Importance of mountain glaciers as a source of dissolved organic carbon. J Geophys Res-Earth 123:2123-2134

Mahowald N, Jickells TD, Baker AR, Artaxo P, Benitez-Nelson CR, Bergametti G, Bond TC, Chen Y, Cohen DD, Herut B, Kubilay N, Losno R, Luo C, Maenhaut W, McGee KA, Okin GS, Siefert RL, Tsukuda S (2008) Global distribution of atmospheric phosphorus sources, concentrations and deposition rates, and anthropogenic impacts. Global Biogeochem Cycles 22:GB4026

McCormick PV, Cairns J (1994) Algae as indicators of environmental change. J Appl Phycol 6:509-526

McMaster, NL (2003) The effects of climate change and nitrogen deposition on the limnology of alpine ponds. Master's thesis, University of Alberta, Edmonton

McMaster NL, Schindler DW (2005) Planktonic and epipelic algal communities and their relationship to physical and chemical variables in alpine ponds in Banff National Park, Canada. Arct Antarct Alp Res 37:337-347

Morris DP, Lewis WM (1988) Phytoplankton nutrient limitation in Colorado mountain lakes. Freshwater Biol 20:315-327

Moser KA, Baron JS, Brahney J, Oleksy IA, Saros JE, Hundley EJ, Sadro SA, Kopáček J, Sommarua R, Kainz MJ, Strecker AL, Chandra S, Walters DM, Preston DL, Michelutti N, Lepori F, Spaulding SA, Christianson KR, Melack JM, Smol JP (2019) Mountain lakes: Eyes on global environmental change. Glob Planet Change 178:77-95

Murphy CA, Thompson PL, Vinebrooke RD (2010) Assessing the sensitivity of alpine lakes and ponds to nitrogen deposition in the Canadian Rocky Mountains. Hydrobiologia 648:83-90

Nanus L, Clow DW, Saros JE, Stephens VC, Campbell DH (2012) Mapping critical loads of nitrogen deposition for aquatic ecosystems in the Rocky Mountains, USA. Environ Pollut 166:125-135

Orihel DM, Schindler DW, Ballard NC, Graham MD, O'Connell DW, Wilson LR, Vinebrooke RD (2015) The "nutrient pump:" Iron-poor sediments fuel low nitrogen-to-phosphorus ratios and cyanobacterial blooms in polymictic lakes. Limnol Oceanogr 60:856-871

Palazzi E, Mortarini L, Terzago S, von Hardenberg J (2019) Elevation‑dependent warming in global climate model simulations at high spatial resolution. Clim Dyn 52:2685-2702

Parmar TK, Rawtani D, Agrawal YK (2016) Bioindicators: the natural indicator of environmental pollution. Bioindicators 9:110-118

Pepin N, Bradley RS, Diaz HF, Baraer M, Caceres ED, Forsythe N, Fowler H, Greenwood G, Hashmi MZ, Liu XD, Miller JR, Ning L, Ohmura A, Palazzi E, Rangwala I, Schöner W, Severskiy I, Shahgedanova M, Wang MB, Williamson SN, Yang D (2015) Elevation-dependent warming in mountain regions of the world. Nat Clim Change 5:424–430

Preston DL, Caine N, McKnight DM, Williams MW, Hell K, Miller MP, Hart SJ, Johnson PTJ (2016) Climate regulates alpine lake ice cover phenology and aquatic ecosystem structure. Geophys Res Lett 43:5353-5360

Reynolds CS (2006) The ecology of freshwater phytoplankton. New York, NY. Cambridge University Press

Roberts JJ, Fausch KD, Schmidt TS, Walters DM (2017) Thermal regimes of Rocky Mountain lakes warm with climate change. PLoS ONE 12:e0179498

Sadro S, Sickman JO, Melack JM, Skeen K (2018) Effects of climate variability on snowmelt and implications for organic matter in a high-elevation lake. Water Resour Res 54:4563-4578

Schindler DW (1987) Detecting ecosystem responses to anthropogenic stress. Can J Fish Aquat Sci 44:6-25

Sickman JO, Melack JM, Clow DW (2003) Evidence for nutrient enrichment of high-elevation lakes in the Sierra Nevada, California. Limnol Oceanogr 48:1885-1892

Slemmons KEH, Saros JE (2012) Implications of nitrogen-rich glacial meltwater for phytoplankton diversity and productivity in alpine lakes. Limnol Oceanogr 57:1651-1663

Slemmons KEH, Saros JE, Simon K (2013) The influence of glacial meltwater on alpine aquatic ecosystems: a review. Environ Sci Processes Impacts 15:1794-1806

Slemmons KEH, Rodgers ML, Stone JR, Saros JE (2017) Nitrogen subsidies in glacial meltwaters have altered planktonic diatom communities in lakes of the US Rocky Mountains for at least a century. Hydrobiologia 800:129-144

Sommaruga R (2015) When glaciers and ice sheets melt: consequences for planktonic organisms. J Plankton Res 37:509-518

Symons CC, Arnott SE, Sweetman JN (2012) Nutrient limitation of phytoplankton communities in Subarctic lakes and ponds in Wapusk National Park, Canada. Polar Biol 35:481-489

Thies H, Nickus U, Mair V, Tessadri R, Tait D, Thaler B, Psenner R (2007) Unexpected response of high alpine lake waters to climate warming. Environ Sci Technol 41:7424-7429

Thompson R, Kamenik C, Schmidt R (2005) Ultra-sensitive alpine lakes and climate change. J Limnol 63:139-152

Vinebrooke RD, Leavitt PR (1998) Direct and indirect effects of allochthonous dissolved organic matter, inorganic nutrients, and ultraviolet radiation on an alpine littoral food web. Limnol Oceanogr 43:1065-1081

Vinebrooke RD, Thompson PL, Hobbs W, Luckman BH, Graham MD, Wolfe AP (2010) Glacially mediated impacts of climate warming on alpine lakes of the Canadian Rocky Mountains. Verh Internat Verein Limnol 30:1449-1452

Vinebrooke RD, MacLennan MM, Bartrons M, Zettel JP (2014) Missing effects of anthropogenic nutrient deposition on sentinel alpine ecosystems. Global Change Biol 20:2173-2182

Vitousek PM, Aber JD, Howarth RW, Likens GE, Matson PA, Schindler DW, Schlesinger WH, Tilman DG (1997) Human alteration of the global nitrogen cycle: sources and consequences. Ecol Appl 7:737-750

Viviroli D, Durr HH, Messerli B, Meybeck M, Weingartner R (2007) Mountains of the world, water towers for humanity: Typology, mapping, and global significance. Water Resour Res 43:W07447

Wang Q, Fan X, Wang M (2014) Recent warming amplification over high elevation regions across the globe. Clim Dyn 43:87-101

Wang X, Parisien M-A, Taylor SW, Candau J-N, Stralberg D, Marshall GA, Little JM, Flannigan MD (2017) Projected changes in daily fire spread across Canada over the next century. Environ Res Lett 12:025005

Williams JJ, Beutel M, Nurse A, Moore B, Hampton SE, Saros JE (2016) Phytoplankton responses to nitrogen enrichment in Pacific Northwest, USA mountain lakes. Hydrobiologia 776:261-276

Williamson CE, Dodds W, Kratz TK, Palmer MA (2008) Lakes and streams as sentinels of environmental change in terrestrial and atmospheric processes. Front Ecol Environ 6:247-254

Woodwell GM (2004) Mountains: Top down. Ambio Special Report 13:35-38

Zhang Z, Goldstein HL, Reynolds RL, Hu Y, Wang X, Zhu M (2018) Phosphorus speciation and solubility in aeolian dust deposition in the interior American West. Envrion Sci Technol 52:2658-2667

Chapter 2 : Concordance of chemically inferred and assayed nutrient limitation of phytoplankton along a depth gradient of alpine lakes in the Canadian Rockies

Introduction

Remote alpine environments are relatively free of local anthropogenic perturbations, making them ideal indicators of the potential impacts of regional events, such as atmospheric wet and dry deposition of pollutants (Williamson et al. 2009; Mladenov et al. 2012; Brahney et al. 2015). Alpine lakes have relatively species-poor food webs, sparse surrounding vegetation, cold temperatures, short growing seasons and dilute nutrient concentrations (Clow and Sueker 2000; Sickman et al. 2003; Vinebrooke and Leavitt 2005; Elser et al. 2009; Bergström et al. 2013). Thus, alpine lakes are expected to be highly responsive to anthropogenic nutrient deposition as it is not readily retained within the surrounding barren landscape (Nanus et al. 2012), prompting concern over the deterioration of water quality, particularly given the prevalence of synergistic responses by freshwater phytoplankton to combined amendments of nitrogen (N) and phosphorus (P; Elser et al. 2007). Although most research has focused on the net effects of N and P on phytoplankton in alpine lakes (e.g. Maberly et al. 2002; Williams et al. 2016; Jacquemin et al. 2018), a knowledge gap exists involving shallower or smaller lentic systems despite these being globally the most abundant type of inland water body (Downing et al. 2006; but see Vinebrooke et al. 2014).

Anthropogenic burning of fossil fuels and use of agricultural fertilizers has greatly increased release of N into the atmosphere, elevating rates of wet N deposition, contained in precipitation, over remote alpine areas (Wolfe et al. 2001; Fenn et al. 2003). The impacts of N deposition in mountain lakes have been monitored more closely in recent years (Elser et al. 2009; Baron et al. 2011; Pardo et al. 2011; Nanus et al. 2012). N deposition has been linked to changes in water chemistry and algal communities, and therefore, also potential deterioration of water quality in high-elevation lakes (Fenn et al. 2003; Sickman et al. 2003; Wolfe et al. 2003). High rates of deposition leading to N-saturation have also been shown to shift phytoplankton from being N- to P-limited (Fenn et al. 2003; Bergström et al. 2008; Elser et al. 2009).

However, the impacts of atmospheric P deposition on alpine lakes have been relatively overlooked compared to those by N deposition. Although mass deposition of P is less than N, the impact of P deposition per unit on lake stoichiometry can be sixteen times greater than that of N deposition (Brahney et al. 2015). Dry deposition of P from aeolian dust has altered nutrient limitation of alpine phytoplankton in the Sierra Nevada Mountains of California (Sickman et al. 2003) and in the Spanish Pyrenees (Camarero and Catalan 2012). Further, P can be deposited as ash as a by-product of fires (Zhang et al. 2002; Brahney et al. 2015), which are predicted to increase in the number of active burning days (Wang et al. 2015). A greater than 50% increase in the number of fire spread days is predicted over the next century in Western Canada (Wang et al. 2017).

N and P are key factors that can limit the growth of freshwater phytoplankton (Reynolds 2006). Dissolved inorganic nitrogen (DIN) often functions as the metric for the bioavailability of N to algae because direct uptake of larger forms of organically bound N is not possible. Total phosphorus (TP) is frequently used because all chemical species of phosphorus are potentially bioavailable, as hydrolytic enzymes (phosphatases) can release phosphorus bound to organic complexes (Bergström 2010). Also, because the DIN:TP responds more directly to atmospheric N deposition than does total N (TN; Bergström 2010), it is a better predictor of nutrient limitation than TN:TP in assessing the effects of nutrient deposition (Morris and Lewis 1988; Bergström 2010). In general, a low DIN:TP predicts N-limitation while high ratios predict P-limitation. We use the thresholds put forth by Morris and Lewis (1988) where DIN:TP mass ratios < 0.5 are predicted to be N-limited, > 4 predicted to be P-limited, and ratios within the range to be co-limited. These thresholds have been frequently used to infer nutrient limitation in mountain lakes in the Canadian Rockies (McMaster and Schindler 2005; Murphy et al. 2010), in the United States Sierra Nevada lakes (Sickman et al. 2003; Sadro et al. 2012; Heard and Sickman 2016), La Caldera high elevation lake in Spain (Medina-Sánchez et al. 2004; García-Jurado et al. 2012). Other threshold values have also been proposed (Bergström 2010; Williams et al. 2017) to infer nutrient limitation and to assess the impacts of atmospheric N deposition (Saros et al. 2010; Baron et al. 2011; Crowley et al. 2012; Jacquemin et al. 2018).

N and P deposition may also alter the community composition of phytoplankton due to differential responses by major algal groups (Reynolds 2006) and species (Sommer 1984) to nutrient availability. For example, N deposition may eliminate the competitive advantage that nitrogen-fixing cyanobacteria otherwise have over other algae under N-limited conditions. Conversely, P deposition may favour diazotrophic cyanobacteria if iron availability and temperature are not limiting (Bergström et al. 2013). Further, P deposition can benefit larger celled chlorophycean species that have greater storage capacity for P, which enables them to dominate certain phytoplankton communities as nutrient concentrations become more dilute during the late summer (Cottingham et al. 1988; Gardner et al. 2008; Teufel et al. 2017; Jacquemin et al. 2018).

The primary objective of this study was to determine how well chemically inferred and experimental lines of evidence of nutrient limitation of phytoplankton support each other along a gradient of deep to shallow lakes situated along the Eastern Front range of the Canadian Rockies. We hypothesized that nutrient limitation of phytoplankton shifts from P- to N-driven with declining water depth based on evidence of shallow and small alpine lakes in the study area having relatively low DIN:TP mass ratios together with N amendments stimulating growth of their phytoplankton and phytobenthos (McMaster 2003; McMaster and Schindler 2005; Murphy et al. 2010; Vinebrooke et al. 2014). Here, the lower water volume would dilute internal loading of P from sediments less than larger mountain lakes, resulting in shallower and smaller waterbodies (i.e. ponds) containing relatively higher concentrations of

P (Vinebrooke et al. 2014). We also expected some evidence of nutrient co-limitation to occur at intermediate DIN:TP mass ratios (0.5 – 4.0) based on meta-analyses showing its prevalence in freshwater ecosystems (Elser et al. 2007; Harpole et al. 2011). Two-factor N × P enrichment bioassays were previously conducted in 2008, where I then analyzed the data to determine the nutrient limitation for 29 lentic ecosystems in this region because these lakes remain relatively understudied for ecological sensitivity to anthropogenic nutrient deposition.

Methods

Field Survey

The alpine study area was located along the Eastern Front range of the Canadian Rockies in Banff National Park (Figure 2.1). Atmospheric N-deposition along the lower foothills east of the Canadian Rockies is an order of magnitude greater than background levels, but still relatively low (~3 kg wet inorganic N ha^{-1} $year^{-1}$; Alberta Environment, unpublished data) compared to that reported elsewhere for lower montane areas, which can range from 13-15 kg N ha^{-1} $year^{-1}$ (Kopáček et al. 2000). Nevertheless, elevated atmospheric N-deposition at lower elevations in the Canadian Rockies highlighted the potential for phytoplankton in the remote alpine backcountry to be affected by N-saturation similar to those communities in lakes already impacted along the Colorado Front Range (Fenn et al. 2003). The 29 sites (Figure 2.1; Table 2.1) were selected based on their fishless, non-glacial status to avoid potential confounding influences of introduced sportfish and glacial flour on nutrient limitation of the phytoplankton (Murphy et al. 2010). All alpine catchments were covered by sparse sedge and heath vegetation amidst predominantly barren rock fields and outcroppings.

In 2008, lakes were accessed via helicopter and on foot in August, and all sampling conducted from an inflatable Alpacka raft positioned at the middle of the waterbody. Water temperature was recorded at 1 m intervals using a YSI submersible probe. A Secchi disk was used to measure light penetration, and the euphotic zone was calculated as double the Secchi depth (Wetzel and Likens 2000). In cases where the calculated euphotic zone was greater than the depth of the lake, it was reported as equalling the maximum depth. A 2 L capacity Van Dorn bottle was used to collect water from the top, middle and bottom of the euphotic zone at each lake and pooled in a 10 L acid-washed cubitainer. For the shallow (< 2 m depth) sites, water was collected from the surface only. One liter of the collected water was filtered onto a Whatman GF/F (0.7 µm) filter to concentrate phytoplankton cells. The filter paper was then immediately folded in half, wrapped in aluminum foil, and stored on ice. A 500 mL aliquot of the filtrate and 2 L of unfiltered water were stored in opaque Nalgene containers on ice for later total dissolved nutrient analysis and total nutrient analysis, respectively. The remaining water from the pooled water sample was passed through a 64 µm stainless steel sieve to remove any large-bodied crustacean zooplankton, and the water was transported via helicopter and truck in 2 L capacity, acid-washed Nalgene containers on ice in a cooler for bioassays within three days of sample collection.

Chemical analyses of total and dissolved nutrients in collected water samples were performed at the University of Alberta Biogeochemical Analytical Service Laboratory using their nationally certified protocols (URL: www.biology.ualberta.ca/basl). A Lachat Quikchem 8500 FIA automated ion analyzer was used to measure the total nitrogen (TN), total dissolved nitrogen (TDN), ammonia (NH_4), and nitrate/nitrite ($NO_3 + NO_2$) with detection limits of 7, 7, 2, and 1 µg L^{-1} respectively. Dissolved organic carbon was measured with a Shimadzu 5000A TOC Analyzer with a detection limit of 0.1 mg L^{-1}. Particulate nitrogen (PN) was measure with an Exeter 440 CHN analyzer. Total phosphorus (TP) and total dissolved phosphorus (TDP) were measured using a Lachat Quikchem 8500 multichannel flow analyzer with a detection limit of 1 µg L^{-1}. The mass of dissolved inorganic nitrogen (DIN) and total phosphorus (TP) in µg were used to calculate the DIN:TP mass ratio.

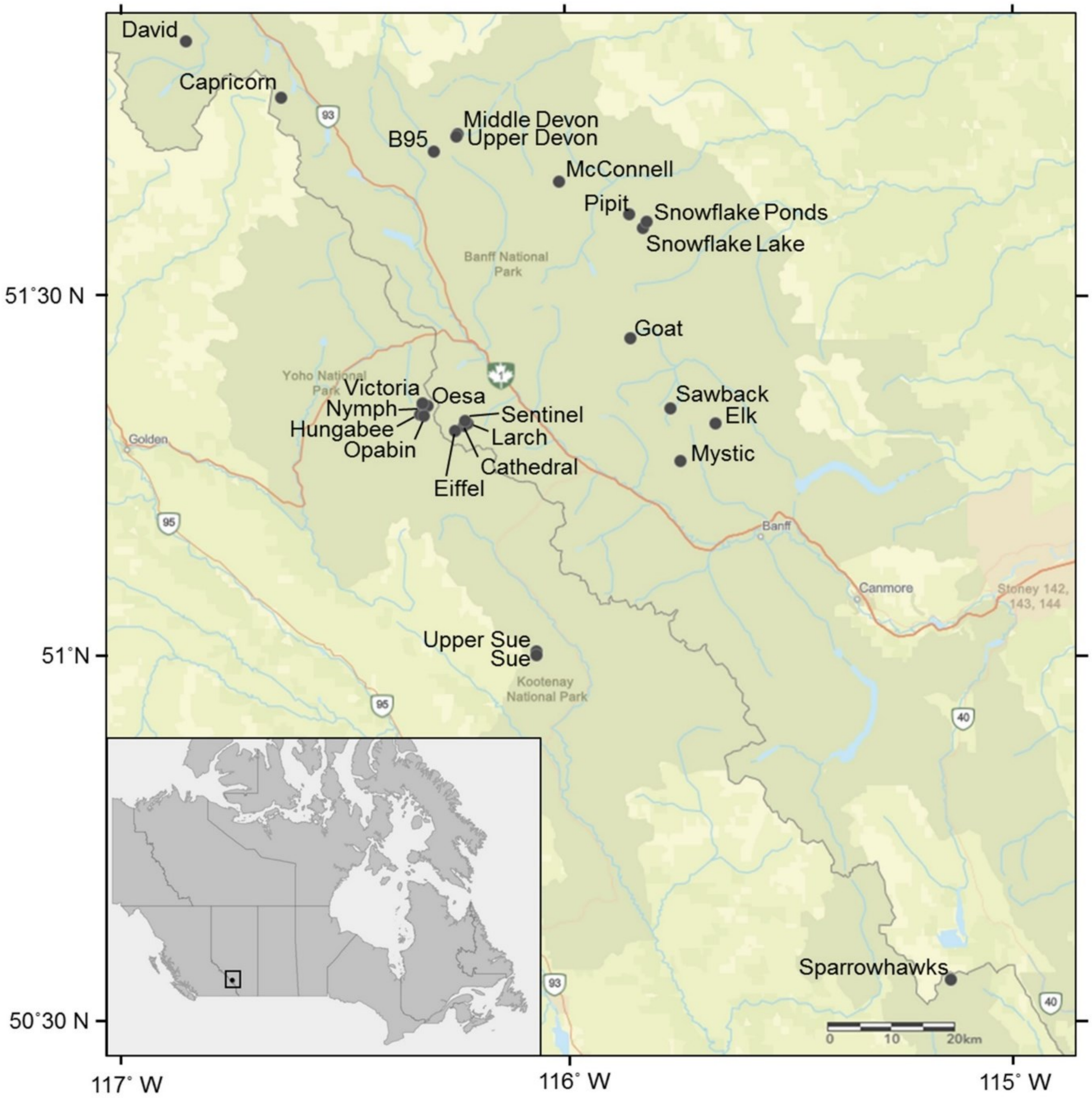

Figure 2.1 Map of the alpine study locations in the Canadian Rocky Mountains.

Table 2.1 Chemical and physical variables for the 29 alpine sites surveyed along the Eastern Front range of the Canadian Rockies.

Site	**Latitude**	**Longitude**	**Elevation (m)**	**Area (m^2)**	**Depth (m)**	**TN ($\mu g\ L^{-1}$)**	**NH_4 ($\mu g\ L^{-1}$)**
B95	51.701954	-116.288943	2400	25300	12.5	249	2
Capricorn	51.772085	-116.626776	2371	327826	8	205	2
Cathedral P	51.328493	-116.225367	2100	38000	1	272	10
David	51.848027	-116.830934	2200	37991	22	170	2
Eiffel	51.32117273	-116.2437963	2300	17142	9.3	121	4
Elk	51.330862	-115.6715	2200	6713	5.8	168	26
Goat	51.44707864	-115.8592225	2438	329427	43	165	9
Hungabee	51.34339722	-116.319354	2100	6230	4	195	8
Larch P	51.3307324	-116.2152474	2393	745	1	139	2
McConnell	51.661813	-116.015577	2390	883	28	178	10
Middle Devon	51.725054	-116.237033	2200	18700	24.1	218	2
Mystic	51.278927	-115.749225	2047	2676	9	102	18
Nymph P	51.356942	-116.314086	2350	231	1	129	2
Oesa	51.35469396	-116.3029872	2285	88450	32	164	8
Opabin	51.34079116	-116.3119414	2234	10200	12.5	163	3
Pipit	51.61721449	-115.8625882	2217	7426	26	185	2
Sawback	51.350941	-115.770141	2045	1725	19.5	142	16
Sentinel	51.33472579	-116.2207633	2423	4053	4	133	4
Snowflake L	51.59860432	-115.8327036	2320	38400	18.5	149	11
Snowflake P 1	51.604497	-115.819594	2290	862	1	789	25
Snowflake P 2	51.599223	-115.815983	2290	191	0.5	307	48
Snowflake P 3	51.597043	-115.807467	2290	151	0.3	319	28
Snowflake P 4	51.602144	-115.799605	2290	NA	1	956	2
Sparrowhawk 1	50.919636	-115.2272085	2698	1953	6.7	40	2
Sparrowhawk 2	50.918612	-115.271142	2649	NA	4.8	447	14
Sue	51.01718	-116.065371	2371	2327	29.5	230	2
Upper Devon	51.722284	-116.241338	2200	444246	24	174	24
Upper Sue	51.012392	-116.066022	2438	57500	4.1	146	2
Victoria	51.35830299	-116.3141925	2225	5750	2.6	199	7

Table 2.1 (continued)

Site	NO_2+NO_3 (μg L^{-1})	TDN (μg L^{-1})	PN (μg L^{-1})	TP (μg L^{-1})	TDP (μg L^{-1})	DOC (mg L^{-1})	DIN:TP	Total Chl (μg L^{-1})
B95	89	209	12	8	4	0.3	11.1	1.4
Capricorn	1	152	9	9	8	0.7	0.3	0.2
Cathedral P	2	215	134	15	3	2.9	0.8	0.2
David	1	130	3	6	2	0.8	0.5	0.3
Eiffel	53	15	43	9	3	0.9	6.3	0.3
Elk	6	69	48	9	6	1	3.6	0.3
Goat	64	63	12	4	4	1	18.3	0.3
Hungabee	15	95	13	3	1	0.8	7.7	0.7
Larch P	66	82	1	5	3	0.5	22	0.2
McConnell	95	82	28	7	3	1.2	15	0.9
Middle Devon	85	213	8	11	3	0.5	7.7	1.2
Mystic	7	110	18	4	3	1.8	6.3	0.4
Nymph P	109	132	16	4	1	0.5	27.2	0.9
Oesa	103	64	20	3	1	0.2	37	0.4
Opabin	41	91	33	4	1	0.3	11	0.2
Pipit	95	96	18	4	1	0.6	23.8	0.3
Sawback	18	73	32	5	2	1.3	6.8	2
Sentinel	36	68	22	6	1	1.3	6.7	0.6
Snowflake L	71	77	33	7	2	0.8	11.7	0.9
Snowflake P 1	6	766	87	42	31	12	0.7	0.7
Snowflake P 2	6	316	61	25	18	6.6	2.2	2.3
Snowflake P 3	5	359	119	20	14	6.1	1.7	0.7
Snowflake P 4	4	890	285	72	55	13.5	0.1	2
Sparrowhawk 1	74	89	76	28	3	1.8	2.6	1.2
Sparrowhawk 2	331	440	40	24	4	0.8	13.8	0.4
Sue	65	65	9	4	4	0.8	16.3	2.7
Upper Devon	14	154	1	4	3	0.5	12.7	2
Upper Sue	1	45	37	2	1	0.8	1.5	1.4
Victoria	102	114	6	1	1	0.2	109	0.1

Abbreviations are total nitrogen (TN), total dissolved nitrogen (TDN), particulate nitrogen (PN), total phosphorus (TP), total dissolved phosphorus (TDP), dissolved organic carbon (DOC), dissolved inorganic nitrogen (DIN). NA represents data were not available. In cases where concentrations were below detection limits, the detection limit was reported.

Nutrient Enrichment Bioassays

To determine the type of nutrient limitation, in 2008, a two-factor (N × P) bioassay was performed in triplicate (n=3) for a total of 12 culture vessels for each of the 29 sites sampled in August. The sieved water was shaken and then transferred into 250 mL vented culture vessels (Corning, USA). Nitrogen additions consisted of 1 mg L^{-1} of N with ammonium nitrate while phosphorus additions involved 30 µg L^{-1} of P with phosphoric acid. Concentrations of nutrients were chosen to double ambient nutrient concentrations. In addition, an equal volume of double deionized water was added to the controls to account for any dilution effect. Hereafter, the four treatment groups will be referred to as C for the control, N for the nitrogen-only, P for the phosphorus-only, and NP for nitrogen combined with phosphorus. Vessels were maintained in a growth chamber (12:12 hour light/dark cycle) at 12˚C for 12 days at an illuminance of 4100 lx using Phillips 44 watts fluorescent lights. Light levels in the growth chamber represented 10% of the solar irradiance, which approximates the light levels near the bottom of the euphotic zone. All vessels were shaken vigorously and repositioned randomly every three days. Logistical constraints involving delivery of water samples for bioassays necessitated a 12-day incubation period after which they were harvested for analysis of phytoplankton pigments by shaking the vessels for 30 seconds and filtering 150 mL onto Whatman GF/F filters. Concentrations of chlorophylls and taxonomically diagnostic xanthophylls (Jeffrey et al. 2005), described below, were determined using high-performance liquid chromatography (HPLC) based on the protocol reported by Vinebrooke and Leavitt (1999). All the nutrient enrichment bioassays and HPLC analyses were performed in 2008.

Statistical Analysis

Using the previously derived pigment concentrations for each nutrient bioassay, I then used two statistical approaches to characterize the nature of nutrient limitation of the pigment-inferred response by the whole phytoplankton community and its major taxonomic groups. Here, chlorophyll *a* was used as a proxy for total phytoplankton community biomass while taxonomically diagnostic pigments were used to estimate the abundance of major algal groups (Vinebrooke and Leavitt 1999; Jeffrey et al. 2005). Specifically, chromophytes were represented by the sum of the representative pigments fucoxanthin, diadinoxanthin, and diatoxanthin. The abundance of chlorophytes was inferred based on the sum of chlorophyll *b*, violaxanthin, neoxanthin, and lutein. Alloxanthin was the representative pigment of cryptophytes. Cyanobacterial abundance was estimated based on the sum of zeaxanthin and canthaxanthin concentrations. First, one-way analysis of variance (ANOVA) was performed on the log-transformed pigment data with Tukey's honest significance difference (HSD) post-hoc test to determine the effects of N and P. Levene's test was used to test the assumption of homogeneity for ANOVA. In cases where the assumption of homogeneity was violated, the Welch's ANOVA with Games-Howell post-hoc test was used. Next, the relative responses (RR) of the entire phytoplankton community and each of its four detected algal groups (chromophytes, chlorophytes, cryptophytes and cyanobacteria) were calculated to normalize the mean pigment response to each of three nutrient amendments (N only, P only, and N plus P) relative to the mean of controls.

$$\mathrm{RR} = \left(\frac{\mathrm{Pigment}_X}{\mathrm{Pigment}_C}\right) \qquad (1)$$

where "Pigment" refers to the concentrations of a specific algal group, and the subscript *X* refers to the N, P, or NP treatment while *C* is the control. Relative responses to the three nutrient amendments were compared using *t*-tests, with a Bonferroni correction, to identify significant differences in response to nutrient additions and to identify how each pigment group differentially responded to nutrient additions. Statistical analyses were performed using SPSS Version 23 with a significance level of $P < 0.05$.

The pigment-based statistical results were used to classify the evidence from the bioassays into the various types of nutrient limitation according to Elser et al. (2009) and Slemmons and Saros (2012).

The response was classed as “no response” if there were no significant responses. In cases of a significant response of N or P greater than the control and no significant difference from the NP treatment, it was deemed “single (*X*) limited” where *X* represents N or P (Figure 2.2a). In cases where both N and P were greater than the control and not significantly different from the NP treatment, the response was classed as “additive dual nutrient limitation”. When both N and P showed significant differences from the control and NP showed a greater significant response than N and P, the response was labelled “synergistic co-limitation” (Figure 2.2b). When the response was only significant when N and P were added together the response was “strict co-limitation” (Figure 2.2c). In cases where only one single nutrient (*X*) was significantly greater than the control, and NP was significantly greater than the response to *X* alone, the limitation type was labelled “sequential co-limitation (*X*)” where *X* is designated as being the primary limiting nutrient (e.g. Elser et al. 2009). For example, in Figure 2.2d, the response of Chl_P is not significant, Chl_N is greater than the control, and combined Chl_{NP} shows the greatest response, indicating a form of primary N-limitation.

The DIN:TP mass ratio and bioassay results for each site were then compared to determine the degree of concordance between chemically inferred and experimentally determined types of nutrient limitation. Here, DIN:TP ratios were compared to expected threshold values proposed by Morris and Lewis (1988) as a basis for inferring the type of nutrient limitation. To enable a clear comparison between the limitation types with the DIN:TP mass ratio predictions, communities classified as single N and sequential co-limitation N were labelled N-limited. Similarly, single P and sequential co-limitation P were grouped as P-limited. Strict co-limitation, synergistic co-limitation and dual limitation were grouped as co-limited. A chi-square goodness of fit test was used to determine if the concordance with the limitation thresholds was significant. Lastly, DIN:TP was related to waterbody depth using regression analysis to determine if the nature of inferred nutrient limitation was a function of waterbody depth (e.g. Murphy et al. 2010).

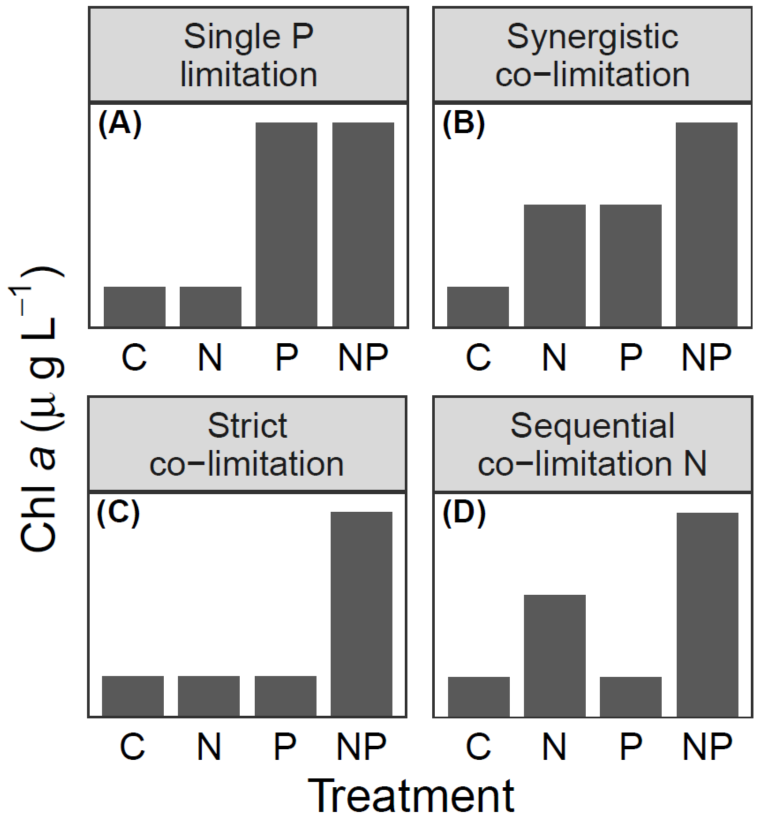

Figure 2.2 An illustration of possible forms of nutrient limitation as defined by Elser et al. (2009). **a** Single P-limitation: a response only to one of the single nutrients. **b** Synergistic co-limitation: a response to both N and P alone, and a greater response when combined. **c** Strict co-limitation: a response only when NP are both added. **d** Sequential co-limitation N: a direct response to N and a greater response to the NP treatment (i.e. a form of primary N-limitation). Limitation types not depicted are dual nutrient limitation: a significant response to N and P alone with no response to NP, and no response: no treatment responses being significantly different from the control.

Results

The measured chemical and physical variables varied considerably among the 29 alpine study sites (Table 2.1). $NO_2 + NO_3$ ranged from 1 to 331 μg L^{-1} and the DIN:TP ranged from 0.1 to 109. The majority of sites had relatively low TP (< 10 μg^{-1}) and DOC (< 2 mg L^{-1}). All sites also contained low total chlorophyll concentrations (< 3 μg L^{-1}), confirming their ultraoligotrophic status. Shallower lake depth was a weak predictor of lower DIN:TP mass ratios (Figure 2.3a; $R^2 = 0.112$, $F_{1,28} = 3.747$, $P = 0.063$).

Phytoplankton communities in most sites were hypothesized to be P-limited while only a few shallower (< 5 m deep) sites were expected to be responsive to N based on the DIN:TP mass ratio thresholds of N-limitation (< 0.5) and P-limitation (> 4) inferred by Morris and Lewis (1988;Table 2.1). However, chemical inferences and bioassays of nutrient limitation agreed in only 16 out of the 29 cases (55%; Figure 2.3b), with a chi-square test revealing the concordance was not significant ($\chi^2 = 1.375$, df = 2, $P = 0.503$). Nine of 19 sites with DIN:TP mass ratios pointing to P-limitation (i.e. > 4) were supported by bioassays showing the same result (47% concordance). However, the DIN:TP ratios did not consistently predict bioassay results of NP co-limitation. Specifically, while DIN:TP ratios in the range of 0.5 – 4.0 were supported by bioassays showing NP co-limitation in five out of seven cases (71% concordance), seven other cases of inferred P-limitation (i.e. DIN:TP > 4) failed to predict the assayed evidence for NP co-limitation (Figure 2.3b). Relatively shallow (< 5 m depth) waterbodies made up 12 of the 29 bioassays. One of these sites showed N-limitation, supporting the chemical inference of these sites being more responsive to N than P. However, bioassays for the other relatively shallow sites showed a variety of responses involving primary P-limitation and strict co-limitation. Two of three sites having DIN:TP mass ratios below 0.5 also showed experimental evidence of N-limitation (67% concordance).

The combined effect of N and P on the chlorophyll *a* concentration was most often synergistic, exceeding the sum of the individual effects of the two nutrients (Figure 2.4; Table 2.2). In all cases of co-limitation, strict co-limitation was the most common form across the study area. Twelve of 29 sites were NP co-limited, with eight communities strictly co-limited, one instance classified as synergistic co-limitation, and three communities showing additive dual limitation. P-limitation was the second most common occurring in 11 of 29 sites. Eight communities were single P-limited and three showed primary P-limitation (sequential co-limitation P). Three of 29 sites were N-limited with two sites showing primary N-limitation (sequential co-limitation N) and only one instance of single N-limitation. Lastly, there were three cases of no chlorophyll response to either N or P amendments.

In most cases, the four major algal groups and chlorophyll *a* responded similarly to the nutrient treatments (Figure 2.5). Chlorophyll *a*, chromophytes and chlorophytes all showed significant relative responses to P alone ($P = 0.0039$, $P < 0.001$, $P = 0.0018$, respectively) that did not differ significantly from their responses to the NP treatment; thereby, indicating strict P-limitation. In comparison, responses by cyanobacteria and cryptophytes to all nutrient treatment combinations were statistically non-significant. However, when considering the response of the algal groups for each site separately, the limitation type varies considerably (Table 2.3). Differences in chlorophyll *a* concentrations among the nutrient amendments matched those for taxonomically diagnostic pigments in 19 cases (66%) for chromophytes, 16 cases (55%) for chlorophytes, six cases for cryptophytes, and five cases for cyanobacteria.

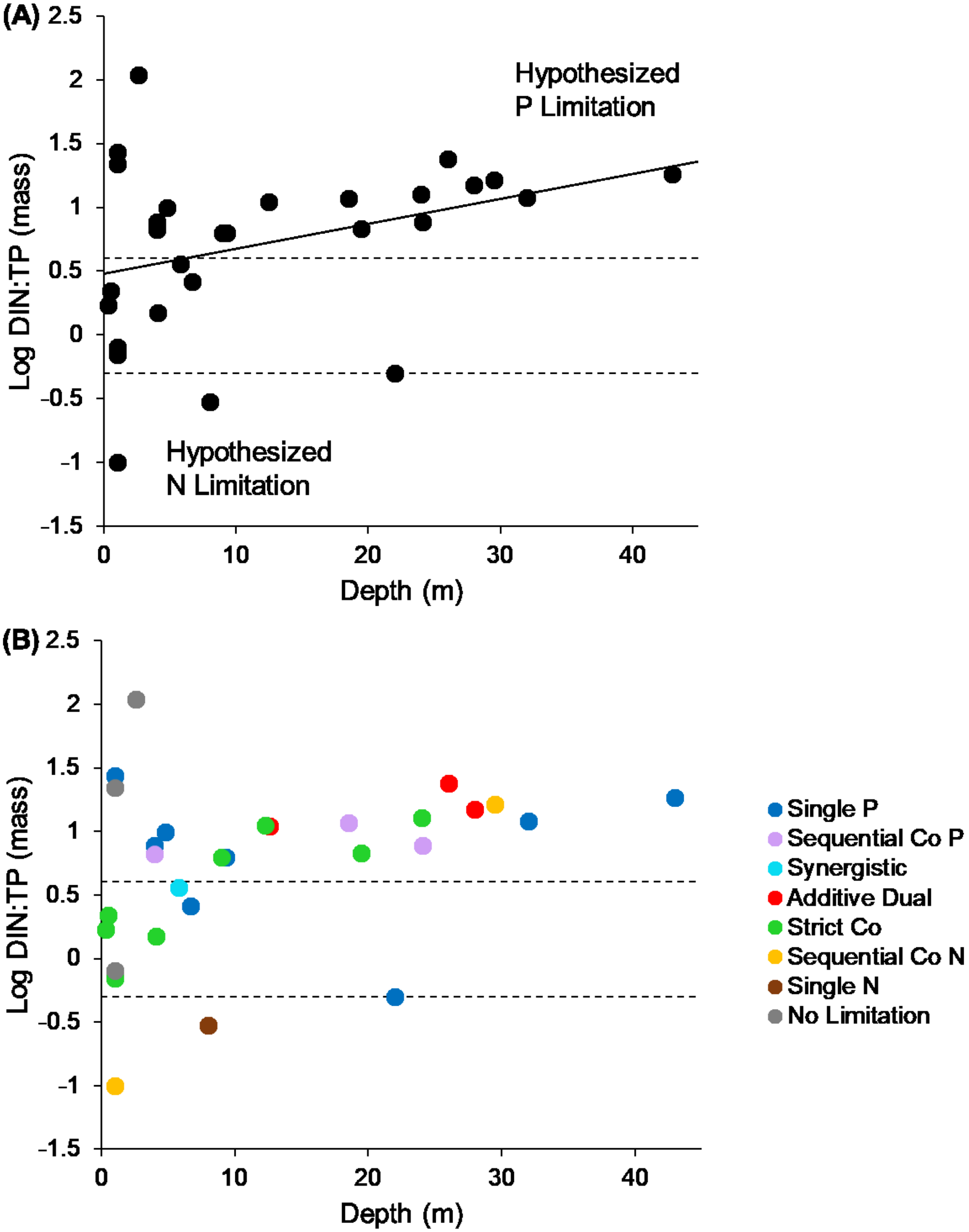

Figure 2.3 The relationship between maximum depth (m) and DIN:TP (μg L^{-1}) for the alpine study sites with the defined nutrient limitation categories. The dotted lines represent predicted DIN:TP mass ratios for N- and P-limitation (Morris and Lewis 1988). **a** shows the predicted limitations and **b** the bioassay results. The solid line indicates a linear trendline.

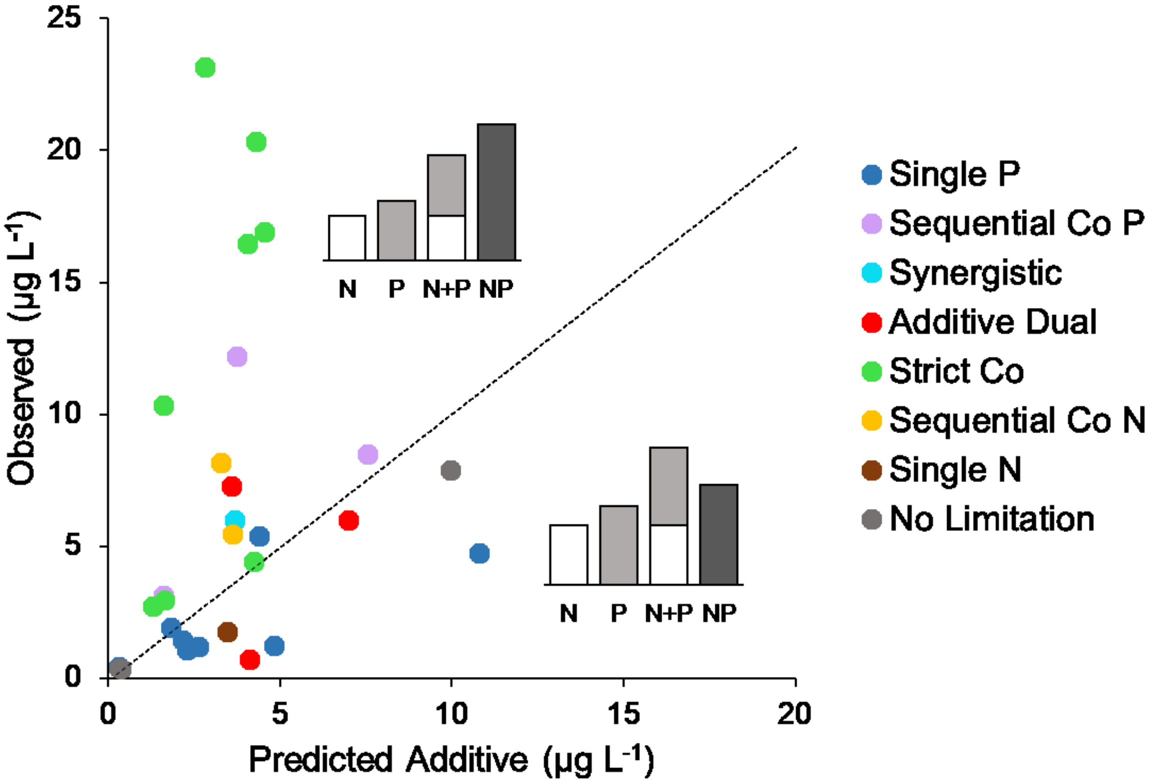

Figure 2.4 The predicted versus observed mean response of chlorophyll *a*. Predicted additive represents the sum of individual chlorophyll *a* responses to N and P treatments while the observed is the actual chlorophyll *a* response to the NP treatment. Dashed line represents 1:1 relationship. Each data point represents the bioassay results from individual study sites (n=29). Points above the dashed line illustrate a synergistic response where the response to NP is greater than the additive response of the single N and P treatments, demonstrated by the upper inset graph. The alternative scenario is demonstrated by the lower inset graph for points below the dashed line.

Table 2.2 Summary of the phytoplankton responses to enrichment with N, P or combined NP, and the statistical results of the ANOVAs used to determine the nutrient limitation type for the 29 alpine study lakes.

Site	**RR-N**	**RR-P**	**RR-NP**	**RR-N/RR-P**	***P* value N effect**	***P* value P effect**	***P* value NP effect**	**Limitation Type**
B95	1.83	2.75	4.80	0.67	0.419	0.091	**0.005**	Strict Co-limitation
Capricorn	104.80	1.96	53.92	53.34	**< 0.0001**	0.993	**< 0.0001**	Single N
Cathedral P	0.86	1.10	1.55	0.78	0.91	0.977	0.193	No Response
David Lake	0.95	11.50	15.27	0.08	1	**< 0.0001**	**< 0.0001**	Single P
Eiffel	0.00	0.00	0.00	0.00	1	**0.046**	0.078	Single P
Elk	2.06	1.88	6.42	1.10	**< 0.0001**	**< 0.0001**	**< 0.0001*** **	Synergistic Co-limitation
Goat	1.07	11.68	3.25	0.09	0.999	**< 0.0001**	**0.003**	Single P
Hungabee	1.18	28.73	14.00	0.04	0.444	**0.023**	**0.444**	Single P
Larch P	1.18	1.35	2.44	0.87	0.989	0.923	0.108	No Response
McConnell	2.99	10.08	11.22	0.30	**0.007**	**< 0.0001**	**< 0.0001**	Additive Dual
Middle Devon	1.46	3.56	5.67	0.41	0.053	**< 0.0001**	**< 0.0001****	Sequential Co-limitation P
Mystic	0.73	3.50	9.02	0.21	0.542	0.392	**0.005**	Strict Co-limitation
Nymph P	2.67	4.91	7.91	0.54	0.117	**0.004**	**< 0.0001**	Single P
Oesa	2.10	45.05	31.40	0.05	0.939	**< 0.0001**	**< 0.0001**	Single P
Opabin	3.38	4.48	16.02	0.75	**0.016**	**0.004**	**0.036**	Additive Dual
Pipit	2.00	2.65	0.81	0.76	**0.026**	**0.003**	**0.832**	Additive Dual
Sawback	1.20	1.47	9.95	0.82	0.852	0.446	**< 0.0001**	Strict Co-limitation
Sentinel	0.56	7.17	25.14	0.08	0.161	**0.028**	**< 0.0001****	Sequential Co-limitation P
Snowflake Lake	1.58	4.91	12.72	0.32	0.876	**0.031**	**< 0.0001****	Sequential Co-limitation P
Snowflake P 1	1.18	1.28	11.69	0.93	0.496	0.232	**< 0.0001**	Strict Co-limitation
Snowflake P 2	1.16	1.35	10.24	0.86	0.659	0.141	**< 0.0001**	Strict Co-limitation
Snowflake P 3	1.15	1.19	19.23	0.97	0.948	0.868	**< 0.0001**	Strict Co-limitation
Snowflake P 4	1.42	0.71	3.22	2.02	**0.007**	0.017	**< 0.0001***	Sequential Co-limitation N
Sparrowhawk 1	1.38	5.09	2.97	0.27	0.118	**< 0.0001**	**< 0.0001**	Single P
Sparrowhawk 2	1.02	4.40	2.38	0.23	0.999	**0.001**	**0.041**	Single P
Sue	2.20	2.52	11.82	0.87	**0.009**	0.063	**0.009***	Sequential Co-limitation N
Upper Devon	1.19	1.49	17.45	0.80	0.544	0.618	**< 0.0001**	Strict Co-limitation
Upper Sue	0.77	0.85	2.99	0.91	0.325	0.574	**0.003**	Strict Co-limitation
Victoria	0.45	3.70	5.33	0.12	0.631	0.096	0.594	No Response

RR-N, RR-P, and RR-NP are the response ratios for the three treatments relative to the unamended control. The relative response to N or P is shown as RR-N/RR-P.

* Denotes the NP treatment was significantly greater than N, ** denotes the NP treatment was significantly greater than P, and *** denotes cases where the NP treatment was significantly greater than both N and P responses. Bolded *P* values are significant ($P < 0.05$) with a positive effect.

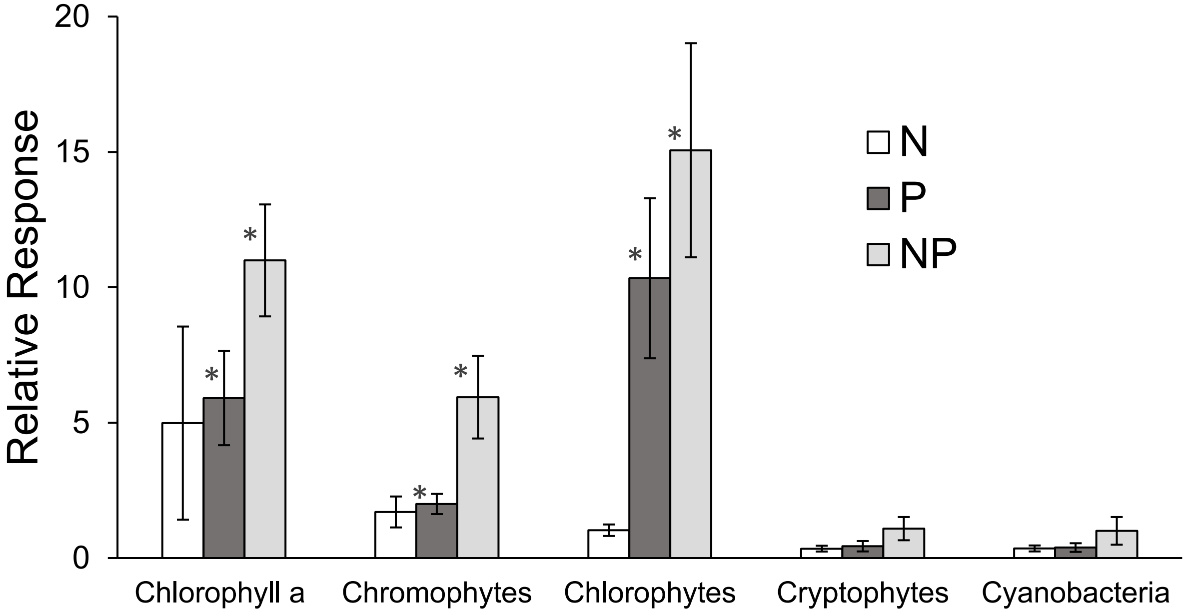

Figure 2.5 The mean relative response (RR) of chlorophyll *a* and four major algal groups (n=29). * indicates significantly greater than the control. Error bars represent standard error.

Table 2.3 Nutrient limitation types for chlorophyll *a* and the four main algal groups of the 29 alpine study sites.

Site	Chlorophyll *a*	Chromophytes	Chlorophytes	Cryptophytes	Cyanobacteria
B95	Strict Co	No Response	Sequential Co P	No Response	No Response
Capricorn	Single N	Single N	No Response	No Response	No Response
Cathedral P	No Response	No Response	Sequential Co P	Strict Co	No Response
David	Single P	Single P	Strict Co	Sequential Co P	No Response
Eiffel	Single P	No Response	Single P	No Response	No Response
Elk	Synergistic Co	Sequential Co N	Synergistic Co	Strict Co	No Response
Goat	Single P	Single P	Single P	No Response	No Response
Hungabee	Single P	Single P	Single P	No Response	No Response
Larch Pond	No Response	No Response	No Response	No Response	No Response
McConnell	Additive Dual	Single P	Single P	Strict Co	No Response
Middle Devon	Sequential Co P	Synergistic Co	Sequential Co P	Strict Co	No Response
Mystic	Strict Co	No Response	Strict Co	No Response	No Response
Nymph	Single P	Single N	No Response	No Response	No Response
Oesa	Single P	Single P	Single P	Single P	No Response
Opabin	Additive Dual	Single N	Synergistic Co	No Response	Sequential Co P
Pipit	Additive Dual	No Response	Additive Dual	No Response	No Response
Sawback	Strict Co	Strict Co	No Response	No Response	No Response
Sentinel	Sequential Co P	Sequential Co P	Sequential Co P	No Response	No Response
Snowflake Lake	Sequential Co P	Sequential Co P	Sequential Co P	Strict Co	No Response
Snowflake P 1	Strict Co	Strict Co	Strict Co	No Response	No Response
Snowflake P 2	Strict Co	Strict Co	Strict Co	Strict Co	Single P
Snowflake P 3	Strict Co	Strict Co	Strict Co	Strict Co	No Response
Snowflake P 4	Sequential Co N	Sequential Co N	Strict Co	Synergistic Co	No Response
Sparrowhawk 1	Single P	Single P	Single P	Single P	No Response
Sparrowhawk 2	Single P	Strict Co	Strict Co	No Response	No Response
Sue	Sequential Co N	Sequential Co N	Strict Co	Strict Co-limitation	No Response
Upper Devon	Strict Co	Strict Co	Strict Co	Sequential Co	Strict Co
Upper Sue	Strict Co	Strict Co	Strict Co	No Response	Strict Co
Victoria	No Response	No Response	No Response	No Response	No Response

Discussion

We found marginal concordance between chemically-inferred and bioassay-based evidence of nutrient limitation of alpine phytoplankton communities from our study area in the Eastern Front range of the Canadian Rockies. The lack of agreement mainly involved cases where DIN:TP mass threshold ratios pointed to P-limitation while bioassays revealed co-limitation by N and P, supporting our hypothesis that phytoplankton would often respond synergistically to the addition of both nutrients. However, our results only provided limited support for the hypothesis of nutrient limitation being a function of lake depth. Although DIN:TP mass ratios were correlated with lake depth, the bioassays did not show the expected shift from P- to N-limitation in the shallower sites. Overall, chlorophytes and chromophytes were the main drivers of whole community responses to the nutrient amendments rather than cyanobacteria or cryptophytes. The demonstrated prevalence of P-driven limitation amongst the tested alpine phytoplankton communities suggests that increased P deposition resulting from recently more frequent and intense wildfires in the Canadian Rockies could stimulate phytoplankton production above treeline. Below, we offer potential explanations for these key findings.

The main reason for only 55% concordance between our DIN:TP- and bioassay-based findings of nutrient limitation involved conflicting results of inferred P-limitation versus experimental co-limitation, respectively. Elsewhere, DIN:TP ratios have also been found to be unreliable predictors of phytoplankton responses to these nutrients in mountain lakes (Slemmons and Saros 2012; Symons et al. 2012; Williams et al. 2016). A possible explanation for this lack of concordance between DIN:TP-based inferences and bioassays of nutrient limitation involves a difference in temporal scale. For example, our use of relatively long 12-day bioassays may have increased the likelihood of co-limitation by better enabling turnover in species that differed in their individual nutrient limitations. Harpole et al. (2011) in their meta-analysis did report that the length of experiment appeared to be a factor of apparent nutrient limitation. In contrast, DIN:TP ratios may better serve as indicators of more short-term physiological rate responses of phytoplankton to nutrients, such as primary productivity. Another potential explanation for the lack of concordance between the two lines of evidence is that DIN:TP is not representative of the potential bioavailability of certain fractions of the dissolved organic nitrogen (DON) pool in mountain lakes (Morris and Lewis 1988; Bunting et al. 2010). Adaptive responses by algae to N-limitation have been shown to involve greater use of DON through up-regulation of genes involved in transport of amino acids, polyamine oxidase, and extracellular proteinases and peptidases (Cooper et al. 2016). Nevertheless, our two lines of evidence for P-limitation did agree in nine out of 11 cases. Similarly, Slemmons and Saros (2012) and Gardner et al. (2008) also found DIN:TP ratios to often be reliable predictors of P-limitation in their bioassays of glacially and non-glacially fed alpine lakes in the central Rocky Mountains, and alpine lakes in the front ranges of the Colorado Rocky Mountains.

Our findings of nutrient co-limitation being widespread across the study area adds to the growing evidence of the ubiquity of synergistic, rather than simply additive, joint effects of N and P on primary producers in freshwater ecosystems (Elser et al. 2007; Allgeier et al. 2011; Harpole et al. 2011; Bracken et al. 2015). More recently, several studies have demonstrated nutrient co-limitation, including lakes in northeast Germany (Kolzau et al. 2014), Lake Baikal in Russia (O'Donnell et al. 2017) a shallow reservoir on the southeast coast of Australia (Müller and Mitrovic 2015). As well, oligotrophic lakes in the Arctic (Levine and Whalen 2001; Ogbebo et al. 2009; Teufel et al. 2017) and high-elevation lakes show evidence of nutrient co-limitation (Morris and Lewis 1988; Sickman et al. 2003; Slemmons and Saros 2012; Bergström et al. 2013; Warner et al. 2017). Potential explanations for synergistic responses by phytoplankton to N plus P range from biochemical to ecological in nature. Such nutrients may have differential effects on both metabolic pathways that interactively stimulate cell growth, and species that vary in their respective limiting nutrient (Harpole et al. 2011). It is also possible that in the presence of both N and P, one nutrient supersedes the other in defining resource limitation, resulting in a net positive effect on algal growth that is greater than the sum of the individual effect of each nutrient (Davidson and Howarth 2007).

Our hypothesis of nutrient limitation being a function of lake depth was minimally supported as the DIN:TP mass ratios were correlated with lake depth but the DIN:TP mass ratios were higher than anticipated for the shallow sites and therefore N-limitation was uncommon. Here, only three experimental sites had a DIN:TP mass ratio less than 0.5, which was fewer than expected based on a previous survey of shallow (< 1 m depth) sites in the Canadian Rockies by McMaster and Schindler (2005). The majority of their 28 shallow study sites had a DIN:TP < 1, predicting N-limitation. A possible explanation for the higher than anticipated DIN:TP mass ratios is that the shallow systems are mixing from wind events, releasing N from the disturbed sediment (Alexander et al. 1989, Luettich et al. 1990). Alpine environments generally have little cover and are subject to strong winds (Billings and Mooney 1968), making mixing events of shallow sites likely. In a nutrient limitation study of lentic systems in the subarctic, Symons et al. (2012) found a higher concentration of nutrients in sites sampled under high wind conditions. Alternatively, the high DIN:TP mass ratios could be a function of catchment characteristics such as the surrounding vegetation. Greater terrestrial vegetation and soil mineralization rates can equate to increased inputs of organic nitrogen, which can thereafter be microbially converted into inorganic forms (Bunting et al. 2010). This could explain the high occurrence of P-limitation in the shallow sites. While the DIN:TP mass ratios were weakly correlated with depth, lake water chemistry has previously been related to catchment characteristics such as slope, catchment area and surrounding vegetation, and local factors including length of ice cover (Kopáček et al. 2000; Kamenik et al. 2001; Marchetto et al. 2009; Bergström et al. 2013). These factors may have been stronger predictors of relative N and P compared to lake depth as originally hypothesized and provide an avenue for future studies in the Canadian Rockies.

The major algal groups exhibited various types of nutrient limitation, occasionally agreeing with the limitation type of the total chlorophyll. The chlorophytes and chromophytes made up the majority of the algal abundance and were often the drivers of the community-level chlorophyll responses to the nutrient treatments. Due to the relatively low cyanobacterial abundance in the treatment amendments and control groups, the chlorophytes were dominant and able to outcompete other taxa for phosphorus due to their larger size and greater storage capacity (Reynolds 2006; Gonzales 2000). The strong response of chlorophytes to enrichments can be due to the dominance of one or a few strongly responding species (Cottingham et al. 1988; Gardner et al. 2008), which may be the case in the current study as well. Our results were similar to Teufel et al. (2017) and Gardner et al. (2008) who found chlorophyte growth accounted for the majority of the phytoplankton growth for the P and NP treatments in bioassays of two oligotrophic lakes in the Antarctic, and an alpine lake in the Colorado front ranges. Diatom abundance (contained within the chromophytes) has been demonstrated to increase from N and NP enrichments in N-limited alpine lakes (Baron et al. 2000; Wolfe et al. 2003). Similarly, Vinebrooke and Leavitt (1998) found a strong response for chrysophytes (contained within the chromophytes) to NP nutrient amendments. Though eutrophication of alpine lakes has occurred elsewhere (Sickman et al. 2003), phytoplankton communities in our study contained few cyanobacteria, which as a group did not exhibit a significant response to either nutrient. Lack of a cyanobacterial response to P amendments potentially involved colder temperatures suppressing their ability to compete against other algal groups by limiting their ability for nitrogen fixation (Tilman et al. 1986). For example, Gallina et al. (2011) found that cyanobacterial biomass was lowest under colder conditions and increased with warmer temperatures in a study of peri-Alpine lakes.

Overall, the bioassay results revealed P-limitation more frequently than N-limitation with 11 P-limited sites and only three N-limited. Phosphorus and nitrogen are considered the primary limiting nutrients for freshwater phytoplankton (Schindler 1974; Elser et al. 1990), with the atmospheric deposition of nutrients affecting the nutrient status of the phytoplankton in some cases. Concern over the effects of external nutrient deposition on the nature of nutrient limitation of lake ecosystems has increased (Elser et al. 1990; Sickman et al. 2003; Bergström et al. 2005; Elser et al. 2009). Some lakes in high-N deposition regions have become saturated with N, increasing the DIN:TP ratios and shifting to P-limitation from their natural N-limited state (Bergström et al. 2005; Bergström and Jansson 2006; Elser et al. 2009). These conclusions have been drawn in general from regions more heavily impacted by anthropogenic deposition of NO_x relative to our study area in the remote backcountry of the Canadian Rockies (Bunting et al. 2010). Thus, we expect that N deposition has not yet elevated DIN:TP ratios in this area enough to account for them being mainly P-limited. Further, historical records indicate that alpine lakes in our study area have remained in their ultraoligotrophic state because of near undetectable concentrations of TP for the past several decades (Loewen et al. 2019).

Our findings of nutrient co-limitation of alpine phytoplankton by N and P being common along the Eastern Front range of the Canadian Rockies highlight the potential for their future synergistic responses to anthropogenic N emissions and wildfires. In general, DIN:TP mass ratios and bioassay results point to the greater relative importance of dry deposition of P from wildfires as being the driver of future changes in phytoplankton communities in this region due to the higher occurrence of P-limitation compared to N. As a caveat, use of DIN:TP to infer phytoplankton threshold responses to N and P could not consistently account for nutrient co-limitation when detected in our study. Therefore, we recommend that future limnological research into the combined effects of N deposition and wildfires on mountain lakes and ponds scale up from nutrient bioassays to more ecologically realistic approaches by conducting whole-ecosystem experiments (e.g. Vinebrooke et al. 2014) and paleolimnological investigations (e.g. Waters et al. 2019).

Literature Cited

Alexander V, Whalen SC, Klingensmith KM (1989) Nitrogen cycling in Arctic lakes and ponds. Hydrobiologia 172:165-172

Allgeier JE, Rosemond AD, Layman CA (2011) The frequency and magnitude of non-additive responses to multiple nutrient enrichment. J Appl Ecol 48:96-101

Baron JS, Rueth HM, Wolfe AM, Nydick KR, Allstott EJ, Minear JT, Moraska B (2000) Ecosystem responses to nitrogen deposition in the Colorado front ranges. Ecosystems 3:352-368

Baron JS, Driscoll CT, Stoddard JL, Richer EE (2011) Empirical critical loads of atmospheric nitrogen deposition for nutrient enrichment and acidification of sensitive US lakes. Bioscience 61:602-613

Bergström A-K (2010) The use of TN:TP and DIN:TP ratios as indicators for phytoplankton nutrient limitation in oligotrophic lakes affected by N deposition. Aquat Sci 72:277-281

Bergström A-K, Blomqvist P, Jansson M (2005) Effects of atmospheric nitrogen deposition on nutrient limitation and phytoplankton biomass in unproductive Swedish lakes. Limnol Oceanogr 50:987-994

Bergström A-K, Jansson M (2006) Atmospheric nitrogen deposition has caused nitrogen enrichment and eutrophication of lakes in the northern hemisphere. Global Change Biol 12:635-643

Bergström A-K, Jonsson A, Jansson M (2008) Phytoplankton responses to nitrogen and phosphorus enrichment in unproductive Swedish lakes along a gradient of atmospheric nitrogen deposition. Aquat Biol 4:55-64

Bergström A-K, Faithful C, Karlsson D, Karlsson J (2013) Nitrogen deposition and warming - effects on phytoplankton nutrient limitation in subarctic lakes. Global Change Biol 19:2557-2568

Billings WD, Mooney HA (1968) The ecology of arctic and alpine plants. Biol Rev 43:481-529

Bracken MES, Hillbrand H, Borer ET, Seabloom EW, Cebrian J, Cleland EE, Elser JJ, Gruner DS, Harpole WS, Ngai JT, Smith JE (2015) Signatures of nutrient limitation and co-limitation: responses of autotroph internal nutrient concentrations to nitrogen and phosphorus addition. Oikos 124:113-121

Brahney J, Mahowald N, Ward DS, Ballantyne AP, Neff JC (2015) Is atmospheric phosphorus pollution altering global alpine lake stoichiometry? Global Biogeochem Cycles 29:1369-1383

Bunting L, Leavitt PR, Weidman RP, Vinebrooke RD (2010) Regulation of nitrogen biogeochemistry of mountain lakes by subsidies of terrestrial dissolved organic matter and the implications for climate studies. Limnol Oceanogr 55:333-345

Camarero L, Catalan J (2012) Atmospheric phosphorus deposition may cause lakes to revert from phosphorus limitation back to nitrogen limitation. Nat Commun 3:1118 DOI: 10.1038/ncomms2125

Clow DW, Sueker JK (2000) Relations between basin characteristics and stream water chemistry in alpine/subalpine basins in Rocky Mountain National Park, Colorado. Water Resour Res 36:49-61

Cooper JT, Sinclair GA, Wawrik B (2016) Transcriptome analysis of Scrippsiella trochoidea CCMP 3099 reveals physiological changes related to nitrate depletion. Frontiers in Micrbiol 7: DOI: 10.3389/fmicb.2016.00639

Cottingham KL, Carpenter SR, St. Amand AL (1988) Responses of epilimnetic phytoplankton to experimental nutrient enrichment in three small seepage lakes. J Plankton Res 20:1889-1914

Crowley KF, McNeil BE, Lovett GM, Canham CD, Driscoll CT, Rustad LE, Denny E, Hallet RA, Arthur MA, Boggs JL, Goodale CL, Kahl JS, McNulty SG, Ollinger SV, Pardo LH, Schaberg PG, Stoddard JL, Weand MP, Weathers KC (2012) Do nutrient limitation patterns shift from nitrogen toward phosphorus with increasing nitrogen deposition across the Northeastern United States. Ecosystems 15:940-957

Davidson EA, Howarth RW (2007) Environmental science: nutrients in synergy. Nature 449:1000-1001

Downing JA, Prairie YT, Cole JJ, Duarte CM, Tranvik LJ, Striegl RG, McDowell WH, Kortelainen P, Caraco NF, Melack JM, Middelburg JJ (2006) The global abundance and size distribution of lakes, ponds, and impoundments. Limnol Oceanogr 51:2388-2397

Elser JJ, Marzolf ER, Goldman CR (1990) Phosphorus and nitrogen limitation of phytoplankton growth in the freshwaters of North America: a review and critique of experimental enrichments. Can J Fish Aquat Sci 47:1468-1477

Elser JJ, Bracken MES, Cleland EE, Gruner DS, Harpole WS, Hillebrand H, Ngai JT, Seabloom EW, Shurin JB, Smith JE (2007) Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. Ecol Lett 10:1135-1142

Elser JJ, Andersen T, Baron JS, Bergström A-K, Jansson M, Kyle M, Nydick KR, Steger L, Hessen DO (2009) Shifts in lake N:P stoichiometry and nutrient limitation driven by atmospheric nitrogen deposition. Science 326:835-837

Fenn ME, Baron JS, Allen EB, Rueth HM, Nydick KR, Geiser L, Bowman WD, Sickman JO, Meixner T, Johnson DW, Neitlich P (2003) Ecological effects of nitrogen deposition in the Western United States. Bioscience 53:404-420

Gallina F, Anneville O, Beniston M (2011) Impacts of extreme air temperatures on cyanobacteria in five deep peri-Alpine lakes. J Limnol 70:186-196

García-Jurado F, de Vicente I, Galotti A, Reul A, Jiménez-Gómez F, Guerrero F (2012) Effects of drought conditions on plankton community and on nutrient availability in an oligotrophic high mountain lake. Arct Antarct Alp Res 44:50-61

Gardner EM, McKnight DM, Lewis WM, Miller MP (2008) Effects of nutrient enrichment on phytoplankton in an alpine lake, Colorado U.S.A. Arct Antarct Alp Res 40:55-64

Gonzales EJ (2000) Nutrient enrichment and zooplankton effects on the phytoplankton community in microcosms from El Andino reservoir (Venezuela). Hydrobiologia 434:81-96

Harpole WS, Ngai JT, Cleland EE, Seabloom EW, Borer ET, Bracken MES, Elser JJ, Gruner DS, Hillebrand H, Shurin JB, Smith JE (2011) Nutrient co-limitation of primary producer communities. Ecol Lett 14:852-862

Heard AM, Sickman JO (2016) Nitrogen assessment points: development and application to high-elevation lakes in the Sierra Nevada, California. Ecosphere 7:e01586

Jacquemin C, Bertrand C, Oursel B, Thorel M, Franquet E, Cavalli L (2018) Growth rate of alpine phytoplankton assemblages from contrasting watershed and N-deposition regimes exposed to nitrogen and phosphorus enrichments. Freshwater Biol 63:1326-1339

Jeffrey SW, Mantoura RFC, Wright SW (2005) Phytoplankton pigments in oceanography: guidelines to modern methods, UNESCO, Madrid

Kamenik C, Schmidt R, Kum G, Psenner R (2001) The influence of catchment characteristics on the water chemistry of mountain lakes. Arct Antarct Alp Res 33:404-409

Kolzau S, Wiedner C, Rucker J, Kohler J, Kohler A, Dolman AM (2014) Seasonal patterns of nitrogen and phosphorus limitation in four German lakes and the predictability of limitation status from ambient nutrient concentrations. PLoS ONE 9:e96065

Kopáček J, Stuchlik E, Straskrabova V, Psenakova P (2000) Factors governing nutrient status of mountain lakes in the Tatra Mountains. Freshwater Biol 369-383

Levine MA, Whalen SC (2001) Nutrient limitation of phytoplankton production in Alaskan Arctic foothill lakes. Hydrobiologia 455:189-201

Loewen CJG, Strecker AL, Larson GL, Vogel A, Fischer J, Vinebrooke RD (2019) Macroecological drivers of zooplankton communities across mountains of western North America. Ecography 42:791- 803

Luettich RA, Harleman DRF, Somlyody L (1990) Dynamic behaviour of suspended sediment concentrations in a shallow lake perturbed by episodic wind events. Limnol Oceanogr 35:1050-1067

Maberly SC, King L, Dent MM, Jones RI, Gibson CE (2002) Nutrient limitation of phytoplankton and periphyton growth in upland lakes. Freshwater Biol 47:2136-2152

Marchetto A, Rogora M, Boggero A, Musazzi S, Lami A, Lotter AF, Tolotti M, Thies H, Psenner R, Massaferro J, Barbieri A (2009) Response of alpine lakes to major environmental gradients, as detected through planktonic, benthic and sedimentary assemblages. Advanc Limnol 62:389-410

McMaster NL (2003) The effects of climate change and nitrogen deposition on the limnology of alpine ponds. Master's thesis, University of Alberta, Edmonton

McMaster NL, Schindler DW (2005) Planktonic and epipelic algal communities and their relationship to physical and chemical variables in alpine ponds in Banff National Park, Canada. Arct Antarc Alp Res 37:337-347

Medina-Sánchez JM, Villar-Argaiz M, Carrillo P (2004) Neither with nor without you: a complex algal control on bacterioplankton in a high mountain lake. Limnol Oceanogr 49:1722-1733

Mladenov N, Williams MW, Schmidt SK, Cawley K (2012) Atmospheric deposition as a source of carbon and nutrients to an alpine catchment of the Colorado Rocky Mountains. Biogeosciences 9:3337-3355

Morris DP, Lewis WM (1988) Phytoplankton nutrient limitation in Colorado Mountain lakes. Freshwater Biol 20:315-327

Müller S, Mitrovic SM (2015) Phytoplankton co-limitation by nitrogen and phosphorus in a shallow reservoir: progression from the phosphorus limitation paradigm. Hydrobiologia 744:255-269

Murphy CA, Thompson PL, Vinebrooke RD (2010) Assessing the sensitivity of alpine lakes and ponds to nitrogen deposition in the Canadian Rocky Mountains. Hydrobiologia 648:83-90

Nanus L, Clow DW, Saros JE, Stephens VC, Campbell DH (2012) Mapping critical loads of nitrogen deposition for aquatic ecosystems in the Rocky Mountains, USA. Environ Pollut 166:125-135

O’Donnell DR, Wilburn P, Silow EA, Yampolsky LY, Litchman E (2017) Nitrogen and phosphorus colimitation of phytoplankton in Lake Baikal: insights from a spatial survey and nutrient enrichment experiments. Limnol Oceanogr 62:1383-1392

Ogbebo FE, Evans MS, Waiser MJ, Tumber VP, Keating JJ (2009) Nutrient limitation of phytoplankton growth in Arctic lakes of the lower Mackenzie River Basin, northern Canada. Can J Fish Aquat Sci 66:247-260

Pardo LH, Fenn ME, Goodale CL, Geiser LH, Driscoll CT, Allen EB, Baron JS, Bobbink R, Bowman WD, Clark CM, Emmett B, Gilliams FS, Greaver TL, Hall SJ, Lilleskov EA, Liu L, Lynch JA, Nadelhoffer KJ, Perakis SS, Robin-Abbott MJ, Stoddard JL, Weathers KC, Dennis RL (2011) Effects of nitrogen deposition and empirical nitrogen critical loads for ecoregions of the United States. Ecol Appl 21:3049-3082

Reynolds CS (2006) The ecology of freshwater phytoplankton. New York, NY. Cambridge University Press

Sadro S, Nelson CE, Melack JM (2012) The influence of landscape position and catchment characteristics on aquatic biogeochemisty in high-elevation lake-chains. Ecosystems 15:363-386

Saros JE, Rose KC, Clow DW, Stephens VC, Nurse AB, Arnett HA, Stone JR, Williamson CE, Wolfe AP (2010) Melting alpine glaciers enrich high-elevation lakes with reactive nitrogen. Environ Sci Technol 44:4891-4896

Schindler DW (1974) Eutrophication and recovery in experimental lakes: implications for lake management. Science 184:897-899

Sickman JO, Melack JM, Clow DW (2003) Evidence for nutrient enrichment of high-elevation lakes in the Sierra Nevada, California. Limnol Oceanogr 48:1885-1892

Slemmons KEH, Saros JE (2012) Implications of nitrogen-rich glacial meltwater for phytoplankton diversity and productivity in alpine lakes. Limnol Oceanogr 57:1651-1663

Sommer U (1984) The paradox of the plankton – Fluctuations of phosphorus availability maintain diversity of phytoplankton in flow-through cultures. Limnol Oceanogr 29:633-636

Symons CC, Arnott SE, Sweetman JN (2012) Nutrient limitation of phytoplankton communities in Subarctic lakes and ponds in Wapusk National Park, Canada. Polar Biol 35:481-489

Teufel AG, Li W, Kiss AJ, Morgan-Kiss, RM (2017) Impact of nitrogen and phosphorus on phytoplankton production and bacterial community structure in two stratified Antarctic lakes: a bioassay approach. Polar Biol 40:1007-1022

Tilman D, Kiesling R, Sterner R, Kilham SS, Johnson FA (1986) Green, bluegreen and diatom algae: taxonomic differences in competitive ability for phosphorus, silicon and nitrogen. Arch Hydrobiol 106:473-485

Vinebrooke RD, Leavitt PR (1998) Direct and interactive effects of allochthonous dissolved organic matter, inorganic nutrients, and ultraviolet radiation on an alpine littoral food web. Limnol Oceanogr 43:1065-1081

Vinebrooke RD, Leavitt PR (1999) Phytobenthos and phytoplankton as potential indicators of climate change in mountain lakes and ponds: a HPLC-based pigment approach. J N Am Benthol Soc 18:15-33

Vinebrooke RD, Leavitt PR (2005) Mountain lakes as indicators of the cumulative impacts of ultraviolet radiation and other environmental stressors. In: Huber UM, Bugmann HKM, Reasoner MA (eds) Global change and mountain regions: An overview of current knowledge. Springer, Dordrecht, Netherlands, pp 437-447

Vinebrooke RD, MacLennan MM, Bartrons M, Zettel JP (2014) Missing effects of anthropogenic nutrient deposition on sentinel alpine ecosystems. Global Change Biol 20:2173-2182

Wang X, Thompson DK, Marshall GA, Tymstra C, Carr R, Flannigan MD (2015) Increasing frequency of extreme fire weather in Canada with climate change. Clim Change 130:573-586

Wang X, Parisien M-A, Taylor SW, Candau J-N, Stralberg D, Marshall GA, Little JM, Flannigan MD (2017) Projected changes in daily fire spread across Canada over the next century. Environ Res Lett 12:025005

Warner KA, Saros JE, Simon KS (2017) Nitrogen subsidies in glacial meltwater: implications of high elevation aquatic chains. Water Resour Res 53:9791-9806

Waters, MN, Metz AP, Smoak JM, Turner H (2019) Chronic prescribed burning alters nutrient deposition and sediment stoichiometry in a lake ecosystem. Ambio 48:672-682

Wetzel RG, Likens G (2000) Limnological analysis. Springer-Verlag, New York

Williams JJ, Beutel M, Nurse A, Moore B, Hampton SE, Saros JE (2016) Phytoplankton responses to nitrogen enrichment in Pacific Northwest, USA mountain lakes. Hydrobiologia 776:261-276

Williams JJ, Lynch JA, Saros JE, Labou SG (2017) Critical loads of atmospheric N deposition for phytoplankton nutrient limitation shifts in western U.S. mountain lakes. Ecosphere 8:e01955

Williamson CE, Saros JE, Schindler DW (2009) Sentinels of change. Science 323:887-888

Wolfe AP, Baron JS, Cornett RJ (2001) Anthropogenic nitrogen deposition induces rapid ecological changes in alpine lakes of the Colorado Front Range (USA). J Paleolimnol 25:1-7

Wolfe AP, Van Gorp AC, Baron JS (2003) Recent ecological and biogeochemical changes in alpine lakes of Rocky Mountain National Park (Colorado, USA): a response to anthropogenic nitrogen deposition. Geobiology 1:153-168

Zhang Q, Carroll JJ, Dixon AJ, Anastasio C (2002) Aircraft measurements of nitrogen and phosphorus in and around the Lake Tahoe basin: Implications for possible sources of atmospheric pollutants to Lake Tahoe. Environ Sci Technol 36:4981-4989

Chapter 3 : Phytoplankton communities as indicators of environmental change and nutrient deposition across an elevational gradient

Introduction

Mountain lakes are considered to be sensitive indicators of regional factors (e.g. climate change, atmospheric pollutants) because they are often located in areas protected from local human disturbances (Vinebrooke and Leavitt 1999a). These lake ecosystems integrate the effects of regional and local factors across entire catchments, making them ideal sentinels of environmental change (Williamson et al. 2008; Adrian et al. 2009). At high elevations, relatively small and oligotrophic alpine lakes with short growing seasons are especially responsive to environmental events (Campbell et al. 2000; Moser et al. 2019). Here, phytoplankton are among the first responders to environmental change because of their relatively small sizes, fast growth rates, and wide dispersal potentials (Schindler 1987; Adrian et al. 2009). Local catchment features can mediate the effects of regional factors on lakes by influencing their biogeochemistry (Kopáček et al. 2000; Kamenik et al. 2001; Sadro et al. 2012). For example, higher elevations are characterized by more precipitation, and steeper slopes, thereby receiving greater deposition of nutrients. Alternatively, lower montane sites have higher concentrations of dissolved organic carbon (DOC) and more vegetated catchments (Moser et al. 2019). A survey of phytoplankton communities along a compressed but large environmental gradient as found in mountains offers an excellent opportunity to study the direct and indirect effects of regional and local factors on lake ecosystems.

The implicit assumption that remote alpine lakes are pristine is being increasingly challenged because of increased wet and dry deposition of nitrogen (N) and phosphorus (P), respectively (Bergström et al. 2008; Elser et al. 2009; Baron et al. 2011; Kopáček et al. 2011; Camarero and Catalan 2012; Brahney et al. 2015; Jacquemin et al. 2019). The burning of fossil fuels and use of agricultural fertilizers has increased atmospheric N, leading to elevated rates of wet N deposition (Wolfe et al. 2001; Fenn et al. 2003). P can be deposited as dry deposition from aeolian dust or as a by-product from wildfires, which are predicted to increase in frequency and magnitude (Zhang et al. 2002; Brahney et al. 2015; Wang et al. 2015). Mountain lakes are sensitive to deposition of nutrients because of their short growing season, steep slopes, sparse vegetation and hydrology dominated by snowmelt (Campbell et al. 2000; Nydick et al. 2003; Moser et al. 2019). The atmospheric nutrient deposition regime can affect the limitation type of the system by altering the N:P mass ratio of the lake, which frequently determines the limiting nutrient (Morris and Lewis 1988; Bergström 2010; Williams et al. 2017). Though some studies have found several mountain lakes to be naturally N-limited (Bergström et al. 2008; Elser et al. 2009), previous work found mountain lakes in the Tatra Mountains (Kopáček et al. 2000), the French Alps (Jacquemin et al. 2018) and the Canadian Rocky Mountains to be primarily P-limited (Chapter 2, Parker et al. 2008). Recent meta-analyses have also demonstrated frequent co-limitation of phytoplankton and the synergistic response to N and P nutrient amendments (Elser et al. 2007; Harpole et al. 2011). Evidence of common synergistic responses from bioassay experiments in alpine lakes (Chapter 2) reveals the possibility of heightened algal growth and potential deterioration of headwaters in the Canadian Rockies.

Mountain lakes and the carbon cycle are both sensitive to climate change, therefore studies assessing changes of DOC within these systems is important (Vinebrooke and Leavitt 1998; Parker et al. 2008; Moser et al. 2019). Increased input of organic carbon due to climate change can involve higher temperatures enhancing decomposition of organic matter in soil (Freeman et al. 2001; Evans et al. 2005), and precipitation flushing DOC into lakes (Weyhenmeyer et al. 2016; Ejarque et al. 2018; Moser et al. 2019). The elevational gradient in DOC concentration could influence the response of alpine versus montane sites to increased input. In high-ultraviolet (UV) systems, such as the alpine, the chromophoric component of DOC functions as a photoprotectant for the phytoplankton (Morris et al. 1995;

Vinebrooke and Leavitt 1999b; Pienitz and Vincent 2000; Sanders et al. 2015). However, the source of DOC will affect the UV attenuation. Allochthonous DOC, entering the lake from runoff in the catchment, is more chromophoric compared to autochthonous DOC, which is produced within the lake, and is nonchromophoric with lower UV absorption. Bacterial and photochemical mineralization of DOC can release organically bound N and P (Vähätalo et al. 2003) and DOC and total phosphorus (TP) are frequently co-exported from the catchment soil (Camarero et al. 2009). DOC enrichment can therefore promote algal production (Klug 2002; Kissman et al. 2013) particularly under warming conditions (Weidman et al. 2014).

Fish introductions into naturally fishless lakes can also stimulate primary production. Previously, widespread fish stocking occurred in numerous lakes in the mountain national parks to increase angling tourism, several of which were naturally fishless (Schindler 2000). Introducing a new, top predator affects the food web and water quality (Leavitt et al. 1994; Schindler and Parker 2002). The introduced fish selectively prey on large, herbivorous zooplankton, releasing smaller and less efficient grazing species from competition (MacLennan et al. 2015; Loewen and Vinebrooke 2016). Phytoplankton can thrive under reduced grazing (Schindler 2000), and due to greater P concentrations being added to the system by fish accessing benthic P, by predating on benthic prey, which was previously unavailable to pelagic communities (Schindler et al. 2001). Warmer temperatures may also interact with fish presence, increasing the nutrient excretion rates by stocked fish under higher temperatures (Vanni 2002). The elevated nutrient availability can promote cyanobacterial growth, particularly in lower elevation montane systems where warmer water temperatures better align with their higher temperature growth optima (O’Neil et al. 2012).

Cyanobacteria can out-compete other algal groups when nutrient concentrations are high (Paerl and Paul 2012; Beaulieu et al. 2013; Taranu et al. 2015). The predicted effects of climate change including warmer temperatures and greater quantities of external deposition of nutrients could favour the bloom- and toxin-forming algal group. Because of higher concentrations of N and P and warmer temperatures, cyanobacteria have increased over the past 200 years, and in greater proportion than other phytoplankton, including a presence in mountain lakes (Brahney et al. 2015; Taranu et al. 2015). Picocyanobacteria (0.2-2 µm) are frequent in oligotrophic mountain lakes and have also been demonstrated to increase under experimental P amendments and warming in northern, high-latitude lakes in subarctic Quebec (Przyulska et al. 2017). Moreover, others have called for greater attention focused on picocyanobacteria in response to climate change (Śliwińska-Wilczewska et al. 2018).

The main goal of this study was to identify the best suite of environmental predictors of mid-summer phytoplankton communities along an elevational gradient consisting of 82 lakes in the Canadian Rocky Mountain National Parks. I hypothesized that nutrients (N and P) and light availability as regulated by DOC would be the key explanatory variables of taxonomic variation across phytoplankton communities. I also expected a positive association between cyanobacterial abundance and higher temperatures and fish presence. A second objective was to chemically infer the nature of nutrient limitation of the surveyed lakes based on their total nitrogen (TN):TP mass ratios and then test these inferences for a subset of 14 high-alpine lakes using nutrient enrichment factorial (N × P) bioassays. Here, I hypothesized that lakes in this region would have remained either P- or NP- co-limited as they had been when last assayed 10 years prior (Chapter 2) as they are located in areas of relatively low nutrient deposition.

Methods

Field Survey

The 82 study lakes are located within a large geographical area within five national mountain parks, including Banff (n = 27), Jasper (n = 25), Waterton (n = 15), Yoho (n = 10) and Kootenay (n = 5; Figure 3.1). The selected sites span a large elevational gradient from 1024 to 2423 m asl, maximum depth from 1.3 to 70.1 m and surface temperature from 1.9 to 19.6 ˚C (Table 3.1; See Appendix A for full data set). GIS-derived catchment features and fish stocking data were obtained from Loewen et al. (2019). Study sites varied in their catchment properties, including area, % bare or vegetated cover and lithography with differences in % mixed sedimentary, % non carbonate sedimentary and % carbonate sedimentary bedrock. Lakes were sampled once, between June 13 to August 24, 2017 or July 17 to August 22, 2018. Lower elevation sites were sampled earlier in the summer, and alpine sites were sampled in August in an effort to control for seasonality effects and timing of ice-off. Fourteen alpine lakes from the survey were selected for nutrient enrichment bioassays, and nutrient limitation was determined following the same protocol as reported in Chapter 2.

From the deepest point of each lake, a portable solid-state submersible YSI probe (sonde) was used to quantify depth profiles in temperature, % dissolved oxygen, pressure, conductivity and pH. A Secchi disk was used to measure light penetration, and the euphotic zone was calculated as double the Secchi depth (Wetzel and Likens 2000). When the calculated photic zone was greater than the depth of the lake, the maximum depth was reported. Depth-integrated water samples were collected from the euphotic zone using tygon tubing. Collected water was pooled in a triple rinsed 10 L cubitainer. 1 L of the pooled water was filtered to concentrate phytoplankton cells onto a Whatman GF/F filter paper. The filter paper was immediately folded in half, wrapped in tinfoil and stored on ice. 500 mL of the filtrate and 500 mL of the pooled unfiltered raw water were collected and stored on ice until later analysis of total dissolved nutrients and total nutrients, respectively.

Chemical analyses of total and dissolved nutrients in collected water samples were performed at the University of Alberta Biogeochemical Analytical Service Laboratory using their nationally certified protocols (URL: www.biology.ualberta.ca/basl). Total nitrogen (TN), total dissolved nitrogen (TDN), total phosphorus (TP) and total dissolved phosphorus (TDP) were analyzed with a Lachat QuickChem QC8500 FIA Automated Ion Analyzer with detection limits of 6, 6, 1 and 2 μg L^{-1}, respectively. Dissolved organic carbon (DOC) was measured with a Shimadzu TOC-5000A Total Organic Carbon Analyzer with a detection limit of 0.1 mg L^{-1}. High-performance liquid chromatography (HPLC) was used to determine concentrations of chlorophylls and taxonomically diagnostic carotenoids (Jeffrey et al. 2005; Table 3.2), based on the protocol reported by Vinebrooke and Leavitt (1999a).

Table 3.1 Summary statistics for environmental, physical and chemical variables from the 82 mountain lakes surveyed in the Canadian Rockies.

	Minimum	**Maximum**	**Mean**	**Median**	**Standard Deviation**
Elevation (m asl)	1024	2423	1653	1582	407
Annual mean air temperature (˚C)	-3.8	4.0	0.1	0.4	2.1
Annual mean precipitation (mm)	468.95	723.98	618.61	631.28	69.05
Mean solar radiation (WH m^{-2})	771269.19	940206.09	859670.10	860084.36	49678.91
Lake area (ha)	0.07	265.04	29.58	10.61	44.10
Catchment area (ha)	2.19	20295.69	1077.65	188.90	2629.28
Catchment area/lake area	2.18	867.79	49.61	20.35	109.03
Vegetation cover (%)	3.25	100.00	64.67	71.89	25.71
Barren land (%)	0.00	93.77	22.75	11.56	26.25
Catchment slope (˚)	0.18	39.47	16.89	15.17	10.94
Mixed sedimentary rock (%)	0.00	100.00	74.16	100.00	41.08
Non-carbonate sedimentary rock (%)	0.00	100.00	19.18	0.00	35.57
Carbonate sedimentary rock (%)	0.00	100.00	6.36	0.00	18.42
Maximum depth (m)	1.3	70.1	14.2	10.5	13.9
Secchi depth (m)	0.5	14	5.4	5.1	3.1
Surface water temperature (˚C)	1.9	19.6	13.8	14.9	4.1
Conductivity (μS^{-cm})	5.80	671.00	208.25	178.60	125.67
TN:TP (mass)	2.61	290.33	38.72	25.78	39.86
TP (μg L^{-1})	1.00	61.00	11.02	8.00	10.65
TDP (μg L^{-1})	1.00	58.00	6.18	3.00	9.54
TN (μg L^{-1})	39	2060	314	189	334
TDN (μg L^{-1})	42	1820	300	167	314
DOC (mg L^{-1})	0.2	16.8	4.1	2.3	3.9
pH	6.40	9.98	8.52	8.41	0.63
Surface dissolved oxygen (%)	59.9	109.7	90.4	90.1	9.5
Fish (presence/absence)	0	1	0.79	1	0.41

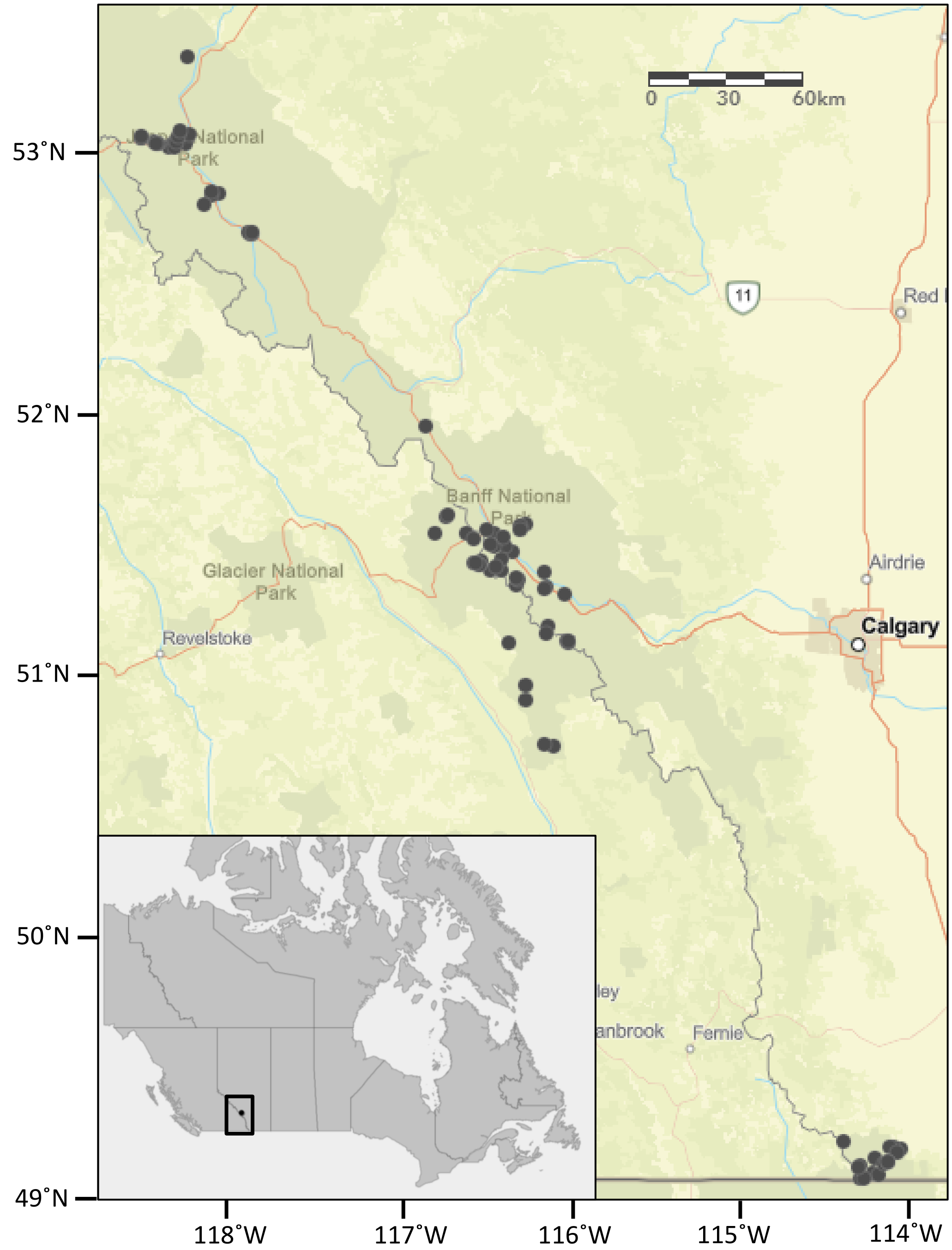

Figure 3.1 Locations of the 82 lakes surveyed within the national mountain parks of Banff, Jasper, Waterton, Kootenay and Yoho, Canada.

Table 3.2 Taxonomically diagnostic carotenoids and chlorophylls from high-performance liquid chromatography (HPLC) and the major algal groups they represent.

Pigment	Algal group
Chlorophyll *a*	All algae
Chlorophyll *b*	Chlorophytes
Alloxanthin	Cryptophytes
Canthaxanthin	Filamentous cyanobacteria
Diadinoxanthin	Chromophytes
Diatoxanthin	Diatoms
Fucoxanthin	Chromophytes (chrysophytes, diatoms and some dinoflagellates)
Lutein	Chlorophytes
Zeaxanthin	All cyanobacteria
Myxoxanthophyll	Colonial cyanobacteria
Violaxanthin	Chlorophytes

Statistical Analysis

Algal abundance

Multiple linear regression with forward selection was performed to identify significant relationships between measured environmental variables on the total algal abundance (total chlorophyll = chlorophyll *a* + chlorophyll *b*). Prior to the regression analysis, a Pearson correlation matrix was used to determine which environmental variables from Table 3.1 were highly collinear. Related environmental variables that violated the assumption of multicollinearity ($r > 0.7$) were removed from the analysis, resulting in the removal of solar irradiance, TDN, TN, TN:TP, catchment area, % bare catchment, % mixed sedimentary, elevation, montane, slope, and air temperature. All remaining variables were included in the analysis.

Community composition

Ordination analyses were conducted to determine the set of chemical and physical variables that best explained variance among the taxonomically diagnostic algal pigments across the surveyed lakes. Preliminary correspondence analysis of the pigment data set revealed that the length of the first ordination axis equalled 2.1 standard deviation units, and therefore the linear method of Redundancy Analysis (RDA) was chosen to further investigate relationships between the pigments and measured environmental variables. Explanatory environmental variables were sequentially eliminated if their variance inflation factor (VIF) was greater than 20, to eliminate highly correlated variables. As a result, TDN, elevation and catchment area were excluded from the RDA. Forward selection was performed on the remaining explanatory variables to determine which variables significantly explain ($P < 0.05$) the phytoplankton community composition. To determine the significance of the axes a Monte Carlo permutation test (n = 999) was used. Prior to all statistical analyses, pigment data were log (1000x + 1) transformed and environmental data, except for pH, were log (x+1) transformed to best improve normality and downweigh the influence of rare or dominant pigments. Pigments that did not contribute more than 1% of total mass in any sample were excluded from the analysis (e.g. neoxanthin). A principal component analysis (PCA) was also performed to determine how much variance is explained by the measured environmental variables. All ordination analyses were performed using Canoco 5 (ter Braak and Smilauer 2012), and regression analyses using SPSS version 23.

Results

Algal Abundance and Nutrient Limitation

Across all 82 surveyed lakes, TP was identified as the only significant predictor of chlorophyll-inferred total algal abundance ($\text{TotChl} = 0.413 + 0.557 \times \text{TP}$; $r^2 = 0.162$, $P < 0.001$). Most lakes contained relatively low concentrations of TP, resulting in TN:TP mass ratios being greater than 25 and predictions of their phytoplankton being P-limited (Table 3.1; Morris and Lewis 1988). In general, the bioassays provided supportive evidence that most of the alpine communities (9 out of 14) responded to the P amendment

(Table 3.3). The mean response of all 14 sites was sequential co-limitation driven by the effect of P (Figure 3.2).

There were five sites that were analyzed using nutrient enrichment bioassays in 2008 (Chapter 2) and performed again in 2018. Eiffel and Sentinel remained in their P-limited state between 2008 and 2018, while Opabin and Osea showed additive dual limitation and single P limitation in 2008, respectively, and were both classified as no response for the 2018 bioassays. Lastly, Hungabee was classified as single P limited in 2008 and showed strict co-limitation in 2018.

Table 3.3 Summary of the phytoplankton responses to enrichment with N, P or combined NP, and the statistical results of the ANOVAs used to determine the nutrient limitation type for the 14 alpine study lakes.

Sites	**RR-N**	**RR-P**	**RR-NP**	**RR-N/RR-P**	***P* value N effect**	***P* value P effect**	***P* value NP effect**	**Limitation type**
Pharaoh	1.26	2.18	2.17	0.58	0.82	**0.02**	**0.021**	Single P
Mummy	1.02	2.32	3.28	0.44	0.99	**< 0.0001**	**< 0.0001****	Sequential Co-limitation P
Oesa	0.48	0.86	1.45	0.56	0.82	0.997	0.823	No Response
Opabin	1.52	1.16	3.23	1.31	0.65	0.902	0.602	No Response
Hungabee	1.11	0.86	3.53	1.29	0.62	0.819	**0.009**	Strict Co-limitation
Mary	1.03	4.82	23.31	0.21	1.00	**< 0.0001**	**< 0.0001****	Sequential Co-limitation P
Rockbound	1.13	2.29	2.74	0.49	0.99	0.056	**0.014**	Strict Co-limitation
Tower	1.16	1.55	11.33	0.75	0.16	**< 0.0001**	**< 0.0001****	Sequential Co-limitation P
Eiffel	0.81	4.61	10.75	0.17	0.99	**0.005**	**< 0.0001**	Sequential Co-limitation P
Sentinel	0.89	5.15	11.24	0.17	0.89	**< 0.0001**	**< 0.0001**	Sequential Co-limitation P
Agnes	0.43	3.19	3.25	0.13	0.03	**0.001**	**0.001**	Single P
Grizzly	1.31	1.02	8.31	1.28	**0.01**	0.984	**< 0.0001***	Sequential Co-limitation N
Laryx	0.97	2.01	17.73	0.48	0.90	**0.011**	**< 0.0001****	Sequential Co-limitation P
Rock Isle	1.30	4.57	6.99	0.28	0.31	**< 0.0001**	**< 0.0001****	Sequential Co-limitation P

RR-N, RR-P, and RR-NP are the response ratios for the three treatments relative to the unamended control. The relative response to N or P is shown as RR-N/RR-P.

* Denotes the NP treatment was significantly greater than N, ** denotes the NP treatment was significantly greater than P. Bolded *P* values are significant ($P < 0.05$) with a positive effect.

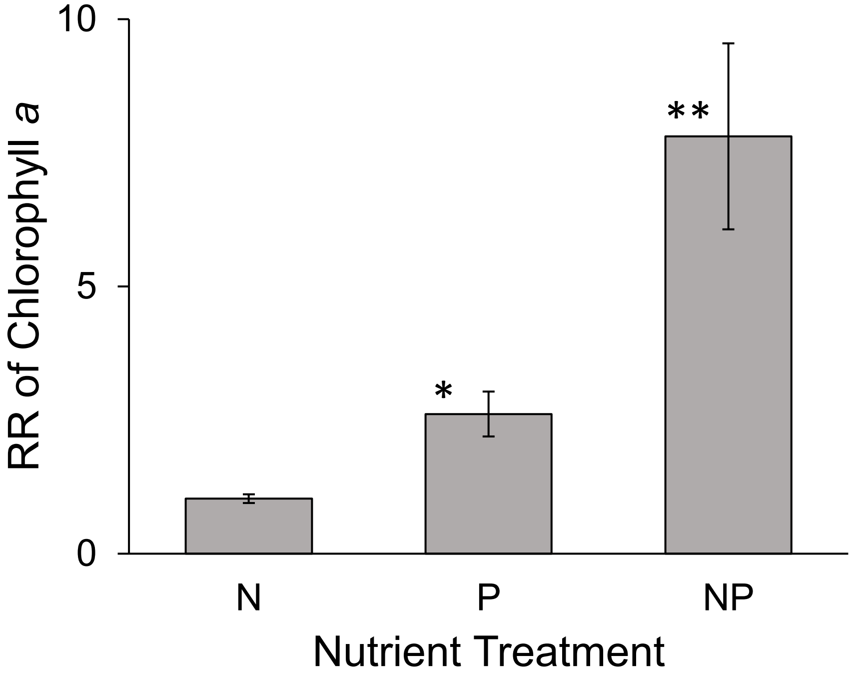

Figure 3.2 The mean relative response (RR) of chlorophyll *a* to nutrient amendments from two factor N × P nutrient enrichments bioassay experiments for (n=14) alpine lakes in the Canadian Rockies. * indicates significantly greater than the control and ** indicates significantly greater than P. Error bars represent standard error.

Community Composition

Based on analysis of algal pigments, phytoplankton communities consisted primarily of chromophytes (fucoxanthin, diadinoxanthin; Figure 3.3). Chlorophytes (chlorophyll *b*, lutein and violaxanthin) were most abundant under low to intermediate concentrations of DOC (Figure 3.3a,b), while cyanobacteria (zeaxanthin), including filamentous forms (canthaxanthin) were more evident at higher DOC concentrations (Figure 3.3c). Colonial cyanobacteria (myxoxanthophyll) were usually not present, except in the three high-DOC lakes. Cryptophytes (alloxanthin) were typically present but represented a small component of the overall community.

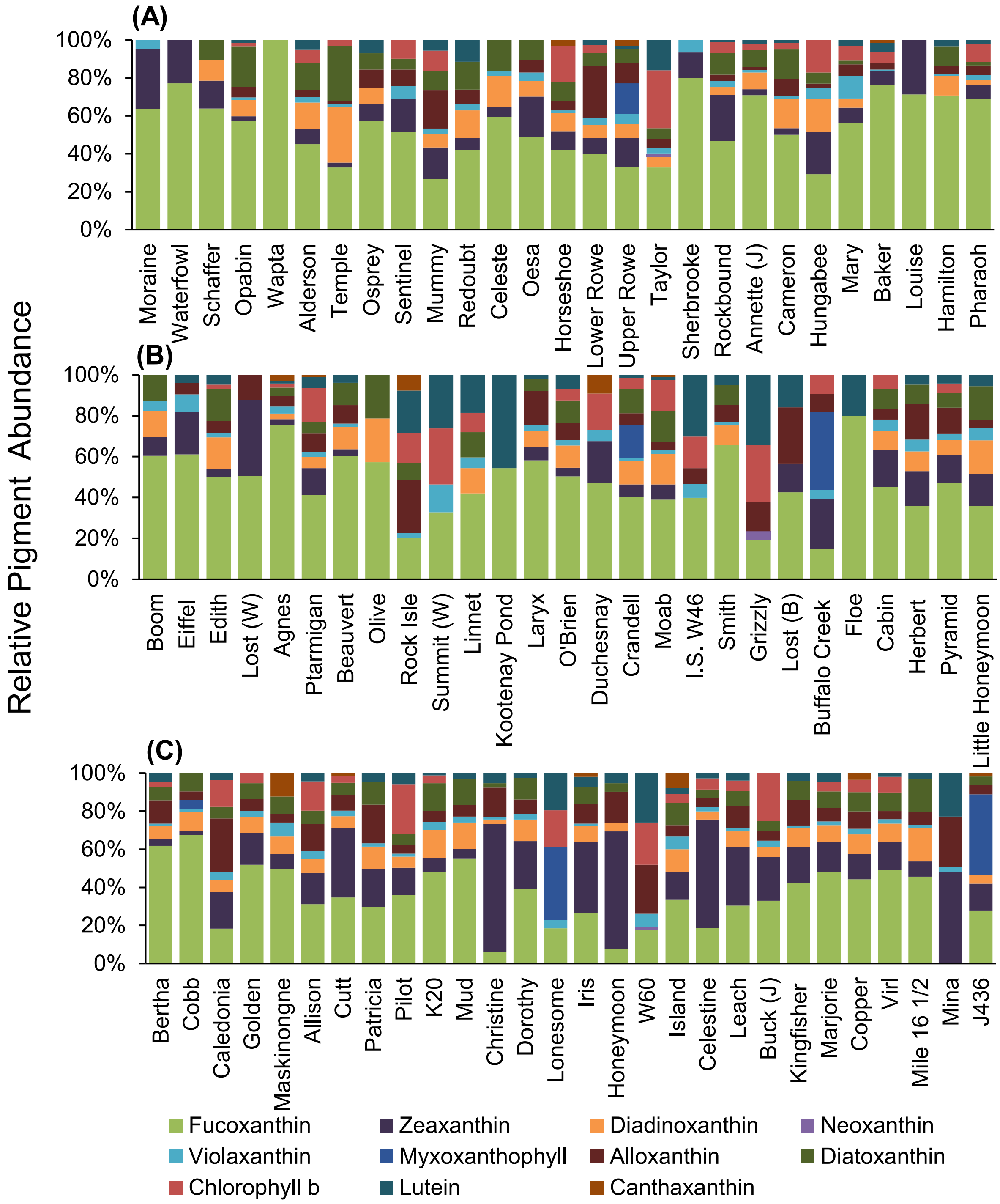

Figure 3.3 Relative abundance of taxonomically diagnostic phytoplankton pigments in 82 mountain lakes along a DOC gradient in the Canadian Rockies. **a** low DOC (< 1 mg L^{-1}) lakes, **b** intermediate DOC (1.1-4.9 mg L^{-1}) lakes, and **c** high DOC (> 5 mg L^{-1}) lakes. The chlorophytes are represented by chlorophyll *b*, lutein, violaxanthin and neoxanthin, the chromophytes by diadinoxanthin and fuxoxanthin. The diatoms are represented by diatoxanthin, the cryptophytes by alloxanthin, and cyanobacteria is represented by zeaxanthin, myxoxanthophyll and canthaxanthin.

DOC, underwater light availability (Secchi depth), % carbonate sedimentary bedrock and % bare catchment best explained variance among the algal pigments across all surveyed lakes (Fig. 3.4; Table 3.4). Forward selection identified DOC as the most significant (*P* = 0.001), followed by Secchi (*P* = 0.002), % carbonate (*P* = 0.025) and % bare catchment (*P* = 0.027). RDA axes 1 and 2 accounted for 14.4% and 2.7% respectively. The first RDA axis was significant (*F* = 13.0, *P* = 0.001), as was the entire ordination (*F* = 4.4, *P* = 0.001). Results from the PCA revealed that axes 1 and 2 explained a total of 58.2% of the variance, which highlights that some potentially important explanatory variables may be missing from the RDA.

RDA axis 1 was best defined by DOC and Secchi depth, which reflected the elevational and trophic (i.e. TP) gradients spanned by the study (Figure 3.4). In general, axis 1 separated sparse alpine and subalpine phytoplankton communities from those that were more diverse at lower elevations primarily based on higher concentrations of cyanobacterial zeaxanthin in the lower montane valley lakes. RDA axis 2 represented a less well-defined gradient of % bare catchment, contrasting chlorophytes (Chl *b*, lutein, violaxanthin) and cyanobacteria (canthaxanthin, myxoxanthophyll) in lakes within relatively barren catchments from diatoms (diatoxanthin, diadinoxanthin) that were more abundant in lake catchments containing greater vegetative cover.

Table 3.4 Significant and independent explanatory variables of variance in taxonomically diagnostic phytoplankton pigments across 82 mountain lakes as identified using forward selection. *P* values are based on 999 Monte Carlo random permutations.

Variable	Abbreviation	Taxonomic variance explained %	*F* value	*P* value
Dissolved organic carbon (mg L^{-1})	DOC	6.7	6.1	0.001
Secchi depth (m)	Secchi	6.4	5.5	0.002
Carbonate sedimentary rock (%)	% Carbonate	2.9	2.7	0.025
Bare catchment (%)	% Bare	2.7	2.6	0.027

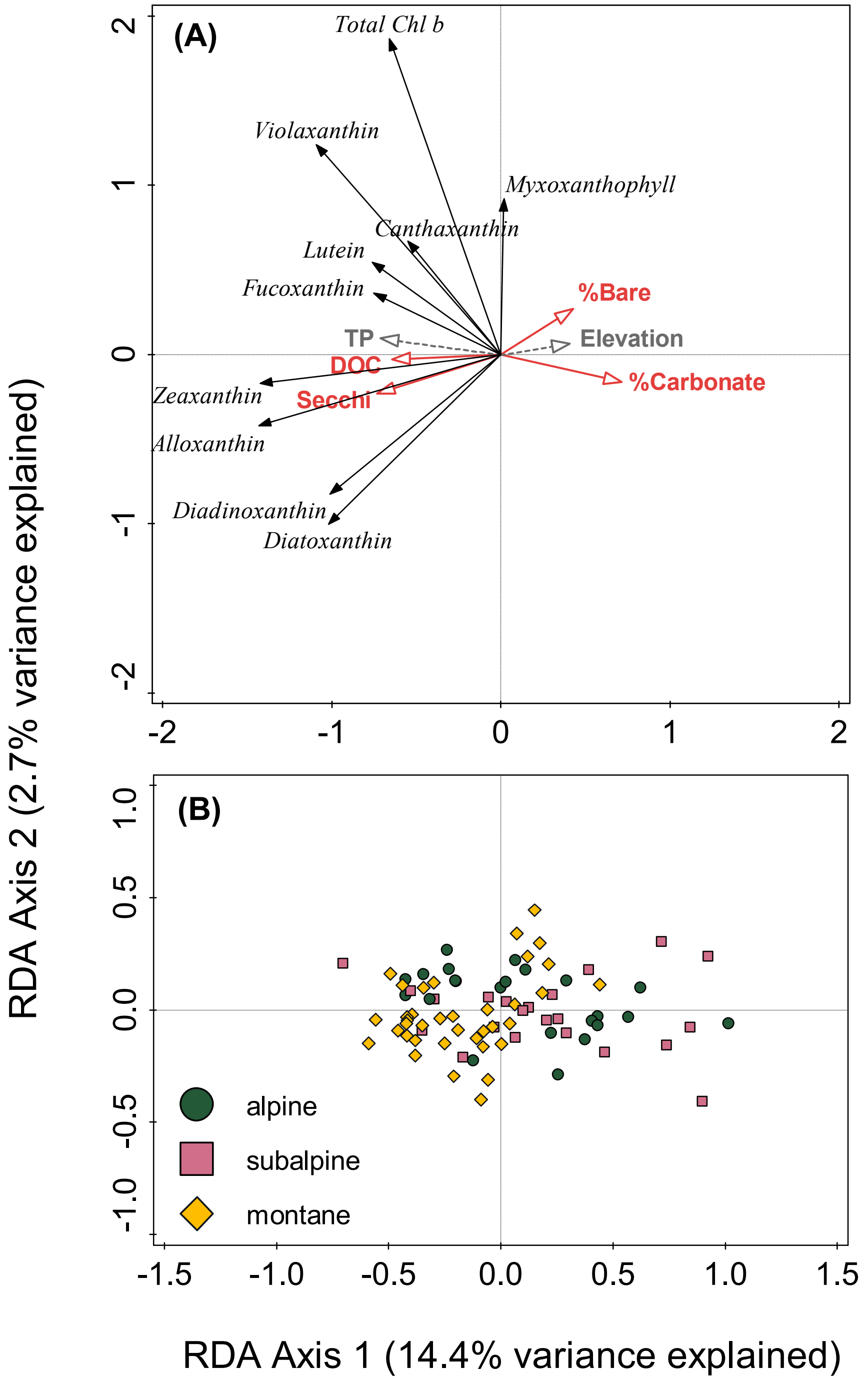

Figure 3.4 Ordination of carotenoids and chlorophyll *b* using a forward selection of **a** explanatory variables that explained a significant amount of variation in the phytoplankton community composition across **b** 82 mountain lakes in the Canadian Rockies along an elevational gradient, based on the redundancy analysis (RDA). Red vectors represent significant explanatory variables while grey vectors show passive supplementary variables. Montane = < 1500 m asl, subalpine = 1500-2000 m asl, alpine = > 2000 m asl. Abbreviations are dissolved organic carbon (DOC) and total phosphorus (TP).

Discussion

TP was the overriding factor both explaining patterns in chlorophyll-inferred phytoplankton biomass across the 82 surveyed lakes and driving most of the alpine phytoplankton responses to experimental nutrient amendments. In contrast, DOC and underwater light availability best explained pigment-inferred taxonomic variation among the surveyed phytoplankton communities. These results also highlighted a greater influence of local catchment heterogeneity (e.g. % barren cover) and water chemistry (e.g. carbonate content) on the algal communities, compared to elevational patterns (i.e. montane, subalpine and alpine). Although fish presence was expected to exert a fertilizing effect on the phytoplankton, it was also not identified as a significant independent predictor of total algal biomass or taxonomic composition. Collectively, my findings suggest that phytoplankton in these study lakes are more directly influenced by changes in local environmental heterogeneity than variation in regional factors (e.g. climate change). In the following paragraphs I will provide potential explanations for these main findings.

Phytoplankton abundance was significantly related to TP (Figure 3.2), supporting both my original hypothesis and findings of previous similar studies conducted in the Canadian Rocky Mountains (McMaster and Schindler 2005). In comparison, N was not identified as a factor of phytoplankton abundance. While N and P are considered the key limiting nutrients for freshwater phytoplankton (Elser et al. 2007), previous nutrient bioassays of phytoplankton from this study area indicated the prevalence of P-limitation (Chapter 2). Most lakes in the current survey had high TN:TP mass ratios predicting P-limitation (Morris and Lewis 1988) and the current bioassays corroborate the finding as most were still primarily P-limited, with an overall synergistic response to N and P, supporting the secondary hypothesis. Phosphorus is a required nutrient for algal growth (Reynolds 2006) and the relationship between total chlorophyll and TP is common (Schindler 1977). The explanation for the occurrence of P-limitation in the Canadian Rocky Mountain lakes remains uncertain. While some regions, such as Sweden, Norway and the Colorado Sierra Nevada have experienced elevated levels of N deposition, resulting in a switch to P-limitation (Bergström et al. 2008; Elser et al. 2009), the Canadian Rockies remain less developed, and likely have not experienced such elevated N deposition (Schindler et al. 2006; Bunting et al. 2010). Lakes in the Canadian Rockies have remained in their oligotrophic state (Loewen et al. 2019), and the prevalence of P-limitation presumably reflects their natural state. However, continuous long-term monitoring of nutrient deposition, and paleolimnological studies interpreting past changes in deposition are required to best understand and predict the response to additional nutrient deposition. Further studies on the different responses of varying algal groups may also be valuable for future predictions (Chapter 2).

Mid-summer phytoplankton pigment composition in the study lakes consisted mainly of fucoxanthin (chrysophytes and some dinoflagellates), followed by high concentrations of chlorophycean pigments (Chl *b*, lutein, violaxanthin; Figure 3.3). Similarly, previous surveys of the study area also identified a dominance of chrysophytes and chlorophytes in mountain lakes (Vinebrooke and Leavitt 1999a; McMaster 2003; Tolotti et al. 2006). The high cellular surface area:volume ratios of chrysophytes allows for relatively fast nutrient uptake, making them well adapted for systems with high N:P ratios (Sandgren 1988; Watson et al. 1997) and to low-nutrient, oligotrophic systems typical of mountain lakes (Tolotti et al. 2003). In addition, the nutritional flexibility of certain chrysophytes (i.e. mixotrophy) is also thought to play a role in their ability to inhabit resource-poor environments (Bird and Kalff 1986). The high TN:TP mass ratio is also favourable to chlorophytes which have a high N optimum (Sandgren 1988).

Cyanobacterial zeaxanthin was closely associated with DOC and Secchi depth. Picocyanobacteria (0.2-2µm) often account for high concentrations of zeaxanthin, especially in dilute and unproductive lakes (Vinebrooke and Leavitt 1999b; Krajewska et al. 2019). Several studies have attempted to find a pattern of picocyanobacterial abundance along a trophic gradient, however, there remains a knowledge-gap in explaining their distribution (Vörös et al. 1998; Callieri and Stockner 2000; Ruber et al. 2016). Unlike mesotrophic conditions that favour most picocyanobacteria in marine systems (Zwirglmaier et al. 2007), certain genera (e.g. *Synechococcus*) are more indicative of clear, oligotrophic freshwater lakes (Vörös et al. 1998; Callieri et al. 2007; Ruber et al. 2016; Watson and Kling 2017; Porcel et al. 2019). Alternatively, others have found that picocyanobacterial distribution responds not only to a trophic gradient, rather there are several potential factors, including grazing pressure, lake residence time and light (Vörös et al. 1998; Callieri and Stockner 2000; Camacho et al. 2003; Watson and Kling 2017). In agreement with my results, DOC was previously found to be significantly related to picocyanobacteria in a large-scale study spanning from Argentinean Patagonia to Maritime Antarctica (Schiaffino et al. 2011), a multi-basin lake in Ontario (Watson and Kling 2017) and to the abundance of benthic cyanobacteria in mountain lakes (Vinebrooke and Leavitt 1999a), suggesting DOC may be a potential resource for picocyanobacteria. It is possible that light availability is also a significant driver of the picocyanobacteria. *Synechococcus* has a sophisticated light-harvesting system, the phycobilisome, allowing growth in differing light regimes, environmental conditions and depths (Vörös et al. 1998; Callieri 2017; Cabello-Yeves et al. 2018). Lastly, DOC was also associated with the lower, montane lakes, which are warmer than the alpine sites, favouring cyanobacteria which require higher temperatures for optimal growth (Reynolds 2006). For example, higher temperatures often favour cyanobacteria over algae as witnessed recently by picocyanobacterial blooms in certain warming lakes (Śliwińska-Wilczewska et al. 2018).

The best predictor of phytoplankton community composition was DOC, which was also partly correlated with underwater light availability (i.e. Secchi depth). DOC across the surveyed lakes appeared to be primarily nonchromophoric in nature. In contrast, DOC concentrations in other lakes often exists as coloured dissolved organic matter (CDOM; Griffin et al. 2018), imparting a brownish appearance to surface waters in which it can act as a photoprotectant against DNA-damaging ultraviolet (UV) radiation

(Vinebrooke and Leavitt 1998; Pienitz and Vincent 2000; Sanders et al. 2015). Importantly, the chromophoric nature, or colour, of DOC indicates its source of origin. DOC from an allochthonous source (e.g. decomposed lignified plant material) is brownish while an autochthonous source (e.g. within-lake algal production) is relatively clear. Moreover, Sommaruga and Augustin (2006) argue that DOC is not an accurate predictor of CDOM in alpine lakes when DOM production is autochthonous. McKnight et al. (1997) found DOC derived from algae in an alpine lake had lower aromaticity and UV absorption because fulvic acids derived from phytoplankton have lower light absorbance than terrestrially derived fulvic acids (McKnight et al. 1994; Martin et al. 2005). Previous research in the Canadian Rocky Mountains also revealed a positive relationship between DOC concentration and Secchi depth providing further support for DOC concentrations in the region being nonchromophoric and autochthonous in nature (Parker et al. 2008).

My results also revealed that chromophycean pigments and cryptophycean alloxanthin were positively associated with DOC. The importance of DOC in promoting algal growth has been reported elsewhere (Weyhenmeyer et al. 2004; Graham and Vinebrooke 2009) by stimulating mixotrophic phytoflagellates, such as certain chrysophytes and cryptophytes (Vinebrooke and Leavitt 1999a). In a factorial (warming × DOC) experiment, Weidman et al. (2014) found that a combination of warming and DOC input resulted in an increase of fucoxanthin. Parker et al. (2008) also found a greater abundance of mixotrophic algae in years of higher DOC, explained by their ability to obtain required nutrients directly from DOC (Rothhaupt 1996). Organically bound N and P can also be mineralized and released from DOC, making the major nutrients bioavailable for algal uptake (Vähätalo et al. 2003). Evidence of allochthonous DOC amendments stimulating larger chlorophytes and colonial chrysophytes (Graham and Vinebrooke 2009) and large cryptophytes (Weyhenmeyer et al. 2004) was attributed to their larger cell size, which enables greater storage capacity of nutrients released from DOC during its photodegradation by solar irradiance. Lastly, my evidence of a positive association between chromophytes and DOC could also be partly explained by how it functions as a carbon source for bacteria, which in turn serve as nutritious prey for certain phagotrophic chrysophytes under otherwise resource-poor conditions (Bird and Kalff 1986).

Catchment features of % bare cover and % carbonate sedimentary bedrock were also identified as explanatory variables of the community composition of mountain phytoplankton. Similarly, a large-scale survey of zooplankton along the North American Cordillera also highlighted the greater importance of local catchment features (land cover and lithology) compared to more regional climatic factors, such as precipitation and temperature for community composition (Loewen et al. 2019). The proportion of bare catchment is generally greater at higher elevations where more harsh environmental conditions suppress vegetation. While the weathering of exposed sedimentary bedrock can be a source of P to lakes, the results from the RDA demonstrate a negative relationship between TP and % bare catchment. Therefore, loading of P into these study lakes is possibly more controlled by soil mineralization than weathering of bare rock. Results from the Tatra Mountains have also demonstrated an inverse relationship between TP and vegetation cover, with TP being lowest at alpine sites (Kopáček et al. 2000). The nutrient concentrations were attributed to vegetation cover representing the pools of soil organic matter (Kopáček et al. 2004). Most sites in the current study had a mixed sedimentary lithology, with only 19 sites containing proportions of carbonate bedrock, most of which also occurred at higher elevations, which are characterized by lower species diversity (Stomp et al. 2011), possibly explaining the negative relationship with most algal pigments.

My analyses lacked zooplankton data that would have enabled exploration of the importance of grazing to the phytoplankton communities, possibly helping explain the low amount of taxonomic variance captured by the RDA. Vinebrooke and Leavitt (1999a) did earlier report that zooplankton biomass was a significant predictor of phytoplankton community composition across mountain lakes and ponds in the Canadian Rockies. Nevertheless, the unexpected lack of significance of fish presence as a predictor of algal biomass or taxonomic composition suggests that trophic interactions affecting the phytoplankton in these mountain lakes are weak. Introduction of sportfish into many of these lakes during the mid-20th century had several negative ramifications on the water quality by increasing phosphorus loading (Schindler et al. 2001) and reducing grazing pressure on the primary producers through the elimination of herbivorous zooplankton (McNaught et al. 1999). Thereafter, Parker et al. (2008) found in four of these alpine lakes that integration of several climatic rather than trophic variables better explained phytoplankton dynamics despite differences in fish-stocking histories among the study lakes.

My findings revealed local water chemistry and associated catchment features to be more important than climate-related factors as predictors of mid-summer phytoplankton community composition in mountain lakes along the Eastern Front range of the Canadian Rockies. The taxonomic variance explained by the factors available was relatively low, which can in part be attributed to the influence of unmeasured environmental variables (e.g. lake flushing rates, glacially derived turbidity) and the importance of seasonality (Reynolds 2006). Nonetheless, the importance of TP to total algal abundance, as well as the prevalence of P-limitation and high TN:TP mass ratios agrees with previous bioassays discussed in Chapter 2. The current study provides further support highlighting the importance of future P deposition from wildfires and the potential impacts of dual nutrient additions, given the strong overall response to NP treatments driving phytoplankton communities.

Interactions between the identified local factors and potential regional variables could result in climate change indirectly affecting mountain phytoplankton communities. Increased melting of glaciers under a warming climate could increase turbidity in lakes while also lowering their temperatures as glacial flour reduces penetration of solar radiation into surface waters (Sommaruga 2015). Further, the expected advancement of treelines to higher elevations would reduce the proportion of bare catchment, possibly leading to increased brownification and warming of alpine lakes situated currently near treelines (Vinebrooke and Leavitt 1998, 2005; Harsch et al. 2009). Clearly, an on-going challenge for limnologists will be to better predict and understand how regional and local factors interact and to determine their cumulative impacts on phytoplankton communities and their functional roles in mountain lakes under a rapidly changing climate.

Literature Cited

Adrian R, O'Reilly CM, Zagarese H, Baines SB, Hessen DO, Keller W, Livingstone DM, Sommaruga R, Straile D, Van Donk E, Weyhenmeyer GA, Winder M (2009) Lakes as sentinels of climate change. Limnol Oceanogr 54:2283-2297

Baron JS, Driscoll CT, Stoddard JL, Richer EE (2011) Empirical critical loads of atmospheric nitrogen deposition for nutrient enrichment and acidification of sensitive US lakes. BioScience 61: 602-613

Beaulieu M, Pick F, Gregory-Eaves I (2013) Nutrients and water temperature are significant predictors of cyanobacterial biomass in a 1147 lakes data set. Limnol Oceangr 58:1736-1746

Bergström A-K (2010) The use of TN:TP and DIN:TP ratios as indicators for phytoplankton nutrient limitation in oligotrophic lakes affected by N deposition. Aquat Sci 72:277-281

Bergström A-K, Jonsson A, Jansson M (2008) Phytoplankton responses to nitrogen and phosphorus enrichment in unproductive Swedish lakes along a gradient of atmospheric nitrogen deposition. Aquat Biol 4:55-64fliteraf

Bird DF, Kalff K (1986) Bacterial grazing by planktonic lake algae. Science 231:493-495

ter Braak CJF, Smilauer P (2012) Canoco Reference Manual and User's Guide: Software for Ordinations (Version 5.0). Microcomputer Power, Ithaca

Brahney J, Mahowald N, Ward DS, Ballantyne AP, Neff JC (2015) Is atmospheric phosphorus pollution altering global alpine Lake stoichiometry? Global Biogeochem Cycles 29:1369-1383

Bunting L, Leavitt PR, Weidman RP, Vinebrooke RD (2010) Regulation of the nitrogen biogeochemistry of mountain lakes by subsidies of terrestrial dissolved organic matter and the implications for climate studies. Limnol Oceanogr 55:333-345

Cabello-Yeves PJ, Picazo A, Camacho A, Callieri C, Rosselli R, Roda-Garcia JJ, Couthino FH, Rodriguez-Valera F (2018) Ecological and genomic features of two widespread freshwater picocyanobacterial. Environ Microbiol 20:3757-3771

Callieri C (2007) Regulation of the nitrogen biogeochemistry of mountain lakes by subsidies of terrestrial dissolved organic matter and the implications for climate studies. Freshwater Reviews 1:1-28

Callieri C (2017) *Synechococcus* plasticity under environmental change. FEMS Microbiol Lett 364:fnx229

Callieri C, Stockner J (2000) Picocyanobacteria success in oligotrophic lakes: fact of fiction? J Limnol 59:72-76

Camacho A, Miracle MR, Vicente E (2003) Which factors determine the abundance and distribution of picocyanobacterial in inland waters? A comparison among different types of lakes and ponds. Arch Hydrobiol 157:321-338

Camarero L, Rogora M, Mosello R, Anderson NJ, Barbieri A, Botev I, Kernan M, Kopáček J, Korhola A, Lotter AF, Muri G, Postolache C, Stuchlik E, Thies H, Wright RF (2009) Regionalisation of chemical variability in European mountain lakes. Freshwater Biol 54:2452-2469

Camarero L, Catalan J (2012) Atmospheric phosphorus deposition may cause lakes to revert from phosphorus limitation back to nitrogen limitation. Nature Communications 3:1118, DOI: 10.1038/ncomms2125

Campbell H, Baron JS, Tonnessen KA, Brooks PD, Schuster PF (2000) Controls on nitrogen flux in alpine/subalpine watersheds of Colorado. Water Resour Res 36:37-47

Ejarque E, Khan S, Steniczka G, Schelker J, Kainz MJ, Battin TJ (2018) Climate-induced hydrological variation controls the transformation of dissolved organic matter in a subalpine lake. Limnol Oceanogr 63:1355-1371

Elser JJ, Bracken MES, Cleland EE, Gruner DS, Harpole WS, Hillebrand H, Ngai JT, Seabloom EW, Shurin JB, Smith JE (2007) Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. Ecol Lett 10:1135-1142

Elser JJ, Anderson T, Baron JS, Bergström A-K, Jansson M, Kyle M, Nydick KR, Steger L, Hessen DO (2009) Shifts in lake N:P stoichiometry and nutrient limitation driven by atmospheric nitrogen deposition. Science 326:835-837

Evans CD, Monteith DT, Cooper DM (2005) Long-term increases in surfaces water dissolved organic carbon: Observations, possible causes and environmental impacts. Environ Pollut 137:55-71

Fenn ME, Baron JS, Allen EB, Rueth HM, Nydick KR, Geiser L, Bowman WD, Sickman JO, Meixner T, Johnson DW, Neitlich P (2003) Ecological effects of nitrogen deposition in the Western United States. BioScience 53:404-420

Freeman C, Evans CD, Monteith DT, Reynolds B, Fenner N (2001) Export of organic carbon from peat soils. Nature 412:785

Graham MD, Vinebrooke RD (2009) Extreme weather events alter planktonic communities in boreal lakes. Limnol Oceanogr 54:2481-2492

Harpole WS, Ngai JT, Cleland EE, Seabloom EW, Borer ET, Bracken MES, Elser JJ, Gruner DS, Hillebrand H, Shurin JB, Smith JE (2011) Nutrient co-limitation of primary producer communities. Ecol Lett 14:852-862

Harsch MA, Hulme PE, McGlone MS, Duncan RP (2009) Are treelines advancing? A global meta-analysis of treeline response to climate warming. Ecol Lett 12:1040-1049

Jacquemin C, Bertrand C, Oursel B, Thorel M, Franquet E, Cavalli L (2018) Growth rate of alpine phytoplankton assemblages from contrasting watersheds and N-deposition regimes exposed to nitrogen and phosphorus enrichments. Freshwater Biol 63:1326-1339

Jacquemin C, Bertrand C, Franquet E, Mounier S, Misson B, Oursel B, Cavalli L (2019) Effects of catchment area and nutrient deposition regime on phytoplankton functionality in alpine lakes. Sci Total Environ 674:114-127

Jeffrey SW, Mantoura RFC, Wright SW (2005) Phytoplankton pigments in oceanography: guidelines to modern methods, UNESCO, Madrid

Kamenik C, Schmidt R, Kum G, Psenner R (2001) The influence of catchment characteristics on the water chemistry of mountain lakes. Arct Antarct Alp Res 33:404-409

Kissman CEH, Williamson CE, Rose KC, Saros JE (2013) Response of phytoplankton in an alpine lake to inputs of dissolved organic matter through nutrient enrichment and trophic forcing. Limnol Oceanogr 58:867-880

Klug JL (2002) Positive and negative effects of allochthonous dissolved organic matter and inorganic nutrients on phytoplankton growth. Can J Fish Aquat Sci 59:85-95

Kopáček J, Stuchlík E, Straškrabová V, Pšenáková P (2000) Factors governing nutrient status of mountain lakes in the Tatra Mountains. Freshwater Biol 43:369-383

Kopáček J, Kaňa J, Šantrůčková H, Picek T, Stuchlík E (2004) Chemical and biological characteristics of alpine soils in the Tatra mountains and their correlation with lake water quality. Water Air Soil Pollut 153:307-327

Kopáček J, Hejzlar J, Vrba J, Stuchlík E (2011) Phosphorus loading of mountain lakes: Terrestrial export and atmospheric deposition. Limnol Oceanogr 56:1343-1354

Krajewska M, Szymczak-Zyla M, Kobos J, Witak M, Kowalewska G (2019) Canthaxanthin in recent sediments as an indicator of heterocystous cyanobacteria in coastal waters. Oceanologia 61:78-88

Leavitt PR, Schindler DE, Paul AJ, Hardie AK, Schindler DW (1994) Fossil pigment records of phytoplankton in trout-stocked alpine lakes. Can J Fish Aquat Sci 51:2411-2423

Loewen CJG, Vinebrooke RD (2016) Regional diversity reverses the negative impacts of an alien predator on local species-poor communities. Ecology 97:2740-2749

Loewen CJG, Strecker AL, Larson GL, Vogel A, Fisher JM, Vinebrooke RD (2019) Macroecological drivers of zooplankton communities across the mountains of western North America. Ecography 42:791-803

MacLennan MM, Dings-Avery C, Vinebrooke RD (2015) Invasive trout increase the climatic sensitivity of zooplankton communities in naturally fishless lakes. Freshwater Biol 60:1502-1513

Martin C, Frenette J-J, Morin J (2005) Changes in the spectral and chemical properties of a water mass passing through extensive macrophyte beds in a large fluvial lake (Lake Saint-Pierre, Québec, Canada). Aquat Sci 67:196-209

McKnight DM, Andrews ED, Spaulding SA, Aiken GR (1994) Aquatic fulvic acids in algal-rich Antarctic ponds. Limnol Oceanogr 39:1972-1979

McKnight DM, Harnish R, Wernshaw RL, Baron JS, Schiff SS (1997) Chemical characteristics of particulate, colloidal, and dissolved organic material in Loch Vale watershed, Rocky Mountain National Park. Biogeochemistry 36:99-124

McMaster, NL (2003) The effects of climate change and nitrogen deposition on the limnology of alpine ponds. Master’s thesis, University of Alberta, Edmonton

McMaster NL, Schindler DW (2005) Planktonic and epipelic algal communities and their relationship to physical and chemical variables in alpine ponds in Banff National Park, Canada. Arct Antarct Alp Res 37:337-347

McNaught AS, Schindler DW, Parker BM, Paul AJ, Anderson RS, Donald DB, Agbeti M (1999) The restoration of an alpine lake food web following fish stocking. Limnol Oceanogr 44:127-136

Morris DP, Zagarese H, Williamson CE, Balseiro EG, Hargreaves BR, Modenutti B, Moeller R, Quimalinos C (1995) The attenuation of solar UV radiation in lakes and the role of dissolved organic carbon. Limnol Oceanogr 40:1381-1391

Morris DP, Lewis WM (1988) Phytoplankton nutrient limitation in Colorado mountain lakes. Freshwater Biol 20:315-327

Moser KA, Baron JS, Brahney J, Oleksy IA, Saros JE, Hundley EJ, Sadro SA, Kopáček J, Sommarua R, Kainz MJ, Strecker AL, Chandra S, Walters DM, Preston DL, Michelutti N, Lepori F, Spaulding SA, Christianson KR, Melack JM, Smol JP (2019) Mountain lakes: Eyes on global environmental change. Glob Planet Change 178:77-95

Nydick KR, Lafrancois BM, Baron JS, Johnson BM (2003) Lake-specific responses to elevated atmospheric nitrogen deposition in the Colorado Rocky Mountains, U.S.A. Hydrobiologia 510:103-114

O'Neil JM, Davis TW, Burford MA, Gobler CJ (2012) The rise of harmful cyanobacteria blooms: The potential roles pf eutrophication and climate change. Harmful Algae 14:313-334

Paerl HW, Paul VJ (2012) Climate change: Links to global expansion of harmful cyanobacteria. Water Research 46:1349-1363

Parker BR, Vinebrooke RD, Schindler DW (2008) Recent climate extremes alter alpine lake ecosystems. PNAS 105:12927-12931

Pienitz R, Vincent WF (2000) Effect of climate change relative to ozone depletion on UV exposure in subarctic lakes. Nature 404:484-487

Porcel S, Saad FJ, Sabio Y Garcia CA, Izaguirre I (2019) Microbial planktonic communities in lakes from a Patagonian basaltic plateau: influence of the water level decrease. Aquat Sci 81:51

Przytulska A, Bartosiewicz M, Vincent WF (2017) Increased risk of cyanobacterial blooms in northern high-latitude lakes through climate warming and phosphorus enrichment. Freshwater Biol 62:1986-1996

Reynolds CS (2006) The ecology of freshwater phytoplankton. New York, NY. Cambridge University Press

Rothhaupt KO (1996) Laboratory experiments with a mixotrophic chrysophyte and obligately phagotrophic and phototrophic competitors. Ecology 77:716–724

Ruber J, Bauer FR, Millard AD, Raeder U, Geist J, Zwirglmaier K (2016) *Synechococcus* diversity along a trophic gradient in the Osterseen Lake District, Bavaria. Microbiology 162:2053-2063

Sadro S, Nelson CE, Melack JM (2012) The influence of landscape position and catchment characteristics on aquatic biogeochemistry in high-elevation lake-chains. Ecosystems 15:363-386

Sanders RW, Cooke SL, Fisher JM, Fey SB, Heinze AW, Jeffrey WH, Macaluso AL, Moeller RE, Morris DP, Neale PJ, Olson MH, Pakulski DJ, Porter JA, Schoener DM, Williamson CE (2015) Shifts in microbial food web structure and productivity after additions of naturally occurring dissolved organic matter: Results from large-scale lacustrine mesocosms. Limnol Oceanogr 60:2130-2144

Sandgren CD (1988) The ecology of chrysophytes flagellates: Their growth and perennation strategies as freshwater phytoplankton. Cambridge, Cambridge University Press.

Schiaffino MR, Unrein F, Gasol JM, Massan R, Balague V, Izaguirre I (2011) Bacterial community structure in a latitudinal gradient of lakes: the role of spatial versus environmental factors. Freshwater Biol 56:1973-1991

Schindler DW (1977) Evolution of phosphorus limitation in lakes. Science 195:260-262

Schindler DW (1987) Detecting ecosystem responses to anthropogenic stress. Can J Fish Aquat Sci 44:6-25

Schindler DW (2000) Aquatic problems caused by human activities in Banff National Park, Alberta, Canada. Ambio 29:401-407

Schindler DE, Knapp RA, Leavitt PR (2001) Alteration of nutrient cycles and algal production resulting from fish introductions into mountain lakes. Ecosystems 4:308–321

Schindler DW, Parker BR (2002) Biological pollutants: Alien fished in mountain lakes. Water Air Soil Pollut 2:379-397

Schindler DW, Dillon PJ, Schreier H (2006) A review of anthropogenic sources of nitrogen and their effects on Canadian aquatic ecosystems. Biogeochemistry 79:25-44

Śliwińska-Wilczewska S, Maculewicz J, Felpeto AB, Latala A (2018) Allelopathic and bloom-forming picocyanobacteria in a changing world. Toxins 10:48

Sommaruga R (2015) When glaciers and ice sheets melt: consequences for planktonic organisms. J Plankton Res 37:509-518

Sommaruga R, Augustin G (2006) Seasonality in UV transparency of an alpine lake is associated to changes in phytoplankton biomass. Aquat Sci 68:129-141

Stomp M, Huisman J, Mittelbach GG, Litchman E, Klausmeier CA (2011) Large-scale biodiversity patterns in freshwater phytoplankton. Ecology 92:2096-2107

Taranu ZE, Grergory-Eaves I, Leavitt PR, Bunting L, Buchaca T, Catalan J, Domaison I, Guilizzoni P, Lami A, McGowan S, Moorhouse H, Morabito G, Frances FR, Stevensen MA, Thompson PL, Vinebrooke RD (2015) Acceleration of cyanobacterial dominance in north temperate-subarctic lakes during the Anthropocene. Ecol Lett 18:375-384

Tolotti M, Thies H, Cantonati M, Hansen CME, Thaler B (2003) Flagellate algae (Chrysophyceae, Dinophyceae, Cryptophyceae) in 48 high mountain lakes of the Northern and Southern slope of the Eastern Alps: biodiversity, taxa distribution and their driving variables. Hydrobiologia 502:331-348

Tolotti M, Manca M, Angeli N, Morabito G, Thaler B, Rott E, Stuchlik E (2006) Phytoplankton and zooplankton associations in a set of alpine high altitude lakes: geographic distribution and ecology. Hydrobiologia 562:99-122

Vähätalo AV, Salonen K, Münster U, Järvinen M, Wetzel RG (2003) Photochemical transformation of allochthonous organic matter provides bioavailable nutrients in a humic lake. Arch Hydrobiol 156:287-314

Vanni MJ (2002) Nutrient cycling by animals in freshwater ecosystems. Annu Rev Ecol Syst 33:341-370

Vinebrooke RD, Leavitt PR (1998) Direct and indirect effects of allochthonous dissolved organic matter, inorganic nutrients, and ultraviolet radiation on an alpine littoral food web. Limnol Oceanogr 43:1065-1081

Vinebrooke RD, Leavitt PR (1999a) Phytobenthos and phytoplankton as potential indicators of climate change in mountain lakes and ponds: a HPLC-based pigment approach. J N Am Benthol Soc 18:15-33

Vinebrooke RD, Leavitt PR (1999b) Differential responses of littoral communities to ultraviolet radiation in an alpine lake. Ecology 80:223-237

Vinebrooke RD, Leavitt PR (2005) Mountain lakes as indicators of the cumulative impacts of ultraviolet radiation and other environmental stressors. In: Huber UM, Bugmann HKM, Reasoner MA (eds) Global change and mountain regions: An overview of current knowledge. Springer, Dordrecht, Netherlands, pp 437-447

Vörös L, Callieri C, Balogh KV, Bertoni R (1998) Freshwater picocyanobacterial along a trophic gradient and light quality range. Hydrobiologia 369/370:117-125

Wang X, Thompson DK, Marshall GA, Tymstra C, Carr R, Flannigan MD (2015) Increasing frequency of extreme fire weather in Canada with climate change. Clim Change 130:573-586

Watson SB, McCauley E, Downing JA (1997) Patterns in phytoplankton taxonomic composition across temperate lakes of differing nutrient status. Limnol Ocreanogr 42:487-495

Watson SB, Kling H (2017) Lake of the Woods phyto- and picoplankton: spatiotemporal patterns in blooms, community composition, and nutrient status. Lake Reserv Manage 33:415-432

Weidman PR, Schindler DW, Thompson PL, Vinebrooke RD (2014) Interactive effects of higher temperature and dissolved organic carbon on planktonic communities in fishless mountain lakes. Freshwater Biol 59:889-904

Weyhenmeyer GA, Willen E, Sonesten L (2004) Effects of an extreme precipitation event on water chemistry and phytoplankton in the Swedish Lake Mälaren. Boreal Environ Res 9:409-420

Weyhenmeyer GA, Müller RA, Norman M, Tranvik LJ (2016) Sensitivity of freshwater to browning in response to future climate change. Clim Change 134:225-239

Williams JJ, Lynch JA, Saros JE, Labou SG (2017) Critical loads of atmospheric N deposition for phytoplankton nutrient limitation shifts in the western U.S. mountain lakes. Ecosphere 8:e01955

Williamson CE, Dodds W, Kratz TK, Palmer MA (2008) Lakes and streams as sentinels of environmental change in terrestrial and atmospheric processes. Front Ecol Environ 6:247-254

Wolfe AP, Baron JS, Cornett RJ (2001) Anthropogenic nitrogen deposition induces rapid ecological changes in alpine lakes of the Colorado Front Range (USA). J Paleolimnol 25:1-7

Zhang Q, Carroll JJ, Dixon AJ, Anastasio C (2002) Aircraft measurements of nitrogen and phosphorus in and around the Lake Tahoe basin: Implications for possible sources of atmospheric pollutants to Lake Tahoe. Environ Sci Technol 36:4981-4989

Zwirglmaier K, Heywood JL, Chamberlain K, Woodward EM, Zubkov MV, Scanlan DJ (2007) Basin-scale distribution patterns of picocyanobacterial lineages in the Atlantic Ocean. Environ Microbiol 9:1278-1290

Chapter 4 : Conclusions

Synthesis

Mountain lakes are chemically dilute which allows phytoplankton to respond readily to even small increases in nutrient content (Schindler 1987; Adrian et al. 2009; Catalan et al. 2013). My research of mountain lakes in the Canadian Rockies showed a greater importance of phosphorus (P), in driving nutrient limitation in alpine lakes and ponds and in explaining total algal abundance across a large elevational gradient. In the ten-year span between samples obtained for Chapter 2 and Chapter 3, the greater importance of P compared to nitrogen (N) remained the same. The results also highlighted a strong synergistic response to the addition of N and P, which has been reported elsewhere (Elser et al. 2007; Harpole et al. 2011). With growing populations, increased land-use development, continued burning of fossil fuels, and the prediction of more wildfires releasing and transporting N and P, the algal communities could be vulnerable to dual nutrient additions.

The ecosystem response to climate change is complex, and phytoplankton may respond differently depending on catchment characteristics, warming rate and nutrient deposition regimes (Bayer et al. 2016; Jacquemin et al. 2019). The large-scale survey of 82 lakes provides evidence that the phytoplankton community composition may be susceptible to indirect effects associated with climate change as well, resulting from the potential advancement of treeline affecting the proportion of bare catchment and DOC input altering light availability. Changes in precipitation patterns, timing of snowmelt and glacier melting could affect nutrient input as well (Sommaruga 2015; Huss et al. 2017). My research highlights that mountain phytoplankton assemblages in the Canadian Rocky Mountain Parks are sensitive to future indirect effects of climate change and increased nutrient deposition which corroborates previous findings within the Canadian Rockies (McMaster and Schindler 2005; Parker et al. 2008; Murphy et al. 2010) and other mountain regions globally (Morales-Baquero et al. 2006; Battarbee et al. 2009; Thies et al. 2012; Bergström et al. 2013). However, there were some shortcomings of the research and together with the results, provide some avenues for future investigations.

Shortcomings

Small-scale bioassay experiments offer the opportunity for several replicates of each treatment, high statistical power and short time frames. Factorial (N × P) nutrient-enrichment bioassays allow for conclusions based on the individual and interactive effects of the two nutrients (Elser et al. 1990). From there, responses can be classified as additive or synergistic which is valuable when predicting the impacts of increased dual nutrient deposition. However, some argue that results from small-scale experiments are not relevant to whole-lake processes because they do not account for changes in nutrient cycling, nutrients released from the sediment, and the succession of algal communities (Carpenter 1996; Schindler 2012). Instead, reliable conclusions should only be drawn from whole-lake experiments (Schindler 2012). There may be a difference between proximate limiting nutrients that will result in immediate algal growth, compared to ultimate limiting nutrients which have a transformative effect on the ecosystem (Vitousek et al. 2010).

The 82-lake survey had a large elevation and geographic span, providing an indication of important broad-scale factors for phytoplankton in the Canadian Rockies. Even with several chemical, physical and environmental factors included in the redundancy analysis, some potentially important variables were unavailable. Zooplankton biomass could have an important impact on the total phytoplankton abundance and preferential grazing can affect the community composition as well (Sterner 1989; Reynolds 2006). Information on whether a lake was glacier-fed or not may also be valuable, along with measures of turbidity. Melting glaciers can have significant effects on algal assemblages (Vinebrooke et al. 2010; Saros et al. 2010; Slemmons et al. 2017), which will be increasingly important with the retreat of mountain glaciers (Fountain et al. 2012; Clarke et al. 2015). Future investigations on the impacts of glacially fed compared to snowmelt fed lakes with a large sample size within the Canadian Rockies would be interesting.

Lastly, while the total N (TN): total P (TP) has been used previously to infer limitation type (Downing and McCauley 1992; Elser et al. 2009), dissolved inorganic nitrogen (DIN) is a better representation of the fraction of N available to the phytoplankton (Morris and Lewis 1988). Therefore, the DIN:TP is frequently a better predictor of limitation type than TN:TP (Morris and Lewis 1988; Bergström 2010). Because of logistical and monetary constraints, we were only able to use TN:TP for inferences of limitation type for the 82-lake survey (Chapter 3). It would have been interesting and allowed for a better comparison with the alpine lakes and ponds used in the bioassays from 2008 (Chapter 2) to have DIN information for the surveyed lakes.

Future Research

Algal pigment data derived using high-performance liquid chromatography (HPLC) can demonstrate changes in algal abundance and community composition, however the taxonomic resolution is limited. Future research of phytoplankton in lakes of the Canadian Rockies to species level would be valuable. These lakes lack a taxonomically comprehensive species inventory of phytoplankton, which would provide valuable baseline data for future biomonitoring efforts. The use of phytoplankton as indicators at the species level is also useful. For example, the diatom species *Asterionella formosa* is responsive to reactive nitrogen and can be used as an indicator of N deposition in alpine lakes (Saros et al. 2005).

The lack of certainty regarding the historical deposition of nutrients and missing estimates of critical load provides another important avenue for future research. Consistent long-term monitoring of nutrient deposition within the national parks, and especially at alpine sites, would be helpful for future studies assessing the impacts of external deposition. By pairing deposition rates with paleolimnological studies, inferences can be made for past ecological responses of diatoms. Previous work in the Colorado front range (Wolfe et al. 2001) and the central US Rocky Mountains (Saros et al. 2003) were able to determine detectable shifts in diatoms in response to elevated anthropogenic N deposition. Paleolimnological studies investigating the past impacts of wildfires in this region and associated changes to algal assemblages and nutrient concentrations would also be an interesting direction for future research.

To better assess the sensitivity of alpine lakes and ponds to nutrient deposition, whole-lake experiments are recommended as another avenue for future research in the Canadian Rockies. A previous attempt to determine the response of phytoplankton to nutrient amendments was complicated by the response of benthic algae and the presence of fairy shrimp (Vinebrooke et al. 2014), demonstrating some of the possible complex ecological interactions when entire lake ecosystems are considered. Further, whole-lake experiments will enable a comparison between the response *in situ* and the bioassay results, determining if the bioassay results represent the proximate or ultimate limiting nutrient (Vitousek et al. 2010) for lakes in the Canadian Rockies. These future avenues of research will continue to contribute to a more comprehensive understanding of the impacts of anthropogenic-induced global changes.

Literature Cited

Adrian R, O'Reilly CM, Zagarese H, Baines SB, Hessen DO, Keller W, Livingstone DM, Sommaruga R, Straile D, Van Donk E, Weyhenmeyer GA, Winder M (2009) Lakes as sentinels of climate change. Limnol Oceanogr 54:2283-2297

Battarbee RW, Kernan M, Rose N (2009) Threatened and stressed mountain lakes of Europe: Assessment and progress. Aquat Ecosyst Health 12:118-128

Bayer TK, Schallenberg M, Burns CW (2016) Contrasting controls on phytoplankton dynamics in low large, pre-alpine lakes imply differential responses to climate change. Hydrobiologia 771:131-150

Bergström A-K (2010) The use of TN:TP and DIN:TP ratios as indicators for phytoplankton nutrient limitation in oligotrophic lakes affected by N deposition. Aquat Sci 72:277-281

Bergström A-K, Faithful C, Karlsson D, Karlsson J (2013) Nitrogen deposition and warming - effects on phytoplankton nutrient limitation in subarctic lakes. Global Change Biol 19:2557-2568

Carpenter SR (1996) Microcosm experiments have limited relevance for community and ecosystem ecology. Ecology 77:677-680

Catalan J, Bartrons M, Camarero L, Grimalt JO (2013) Mountain waters as witnesses of global pollution. In: Pechan P, de Vries GE (eds) Living with water: Targeting quality in a dynamic world. Springer, New York, pp 31-67

Downing JA, McCauley E (1992) The nitrogen: phosphorus relationship in lakes. Limnol Oceanogr 37:936-945

Elser JJ, Marzolf ER, Goldman CR (1990) Phosphorus and nitrogen limitation of phytoplankton growth in the freshwaters of North America: a review and critique of experimental enrichments. Can J Fish Aquat Sci 47:1468-1477

Elser JJ, Bracken MES, Cleland EE, Gruner DS, Harpole WS, Hillebrand H, Ngai JT, Seabloom EW, Shurin JB, Smith JE (2007) Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. Ecol Lett 10:1135-1142

Elser JJ, Anderson T, Baron JS, Bergström A-K, Jansson M, Kyle M, Nydick KR, Steger L, Hessen DO (2009) Shifts in lake N:P stoichiometry and nutrient limitation driven by atmospheric nitrogen deposition. Science 326:835-837

Harpole WS, Ngai JT, Cleland EE, Seabloom EW, Borer ET, Bracken MES, Elser JJ, Gruner DS, Hillebrand H, Shurin JB, Smith JE (2011) Nutrient co-limitation of primary producer communities. Ecol Lett 14:852-862

Huss M, Bookhagen B, Huggel C, Jacobsen D, Bradley RS, Clague JJ, Vuille M, Buytaert W, Cayan DR, Greenwood G, Mark BG, Miler AM, Weingartner R, Winder M (2017) Toward mountains without permanent snow and ice. Earth's Future 5:418-435

Jacquemin C, Bertrand C, Franquet E, Mounier S, Misson B, Oursel B, Cavalli L (2019) Effects of catchment area and nutrient deposition regime on phytoplankton functionality in alpine lakes. Sci Total Environ 674:114-127

McMaster NL, Schindler DW (2005) Planktonic and epipelic algal communities and their relationship to physical and chemical variables in alpine ponds in Banff National Park, Canada. Arct Antarct Alp Res 37:337-347

Morales-Baquero R, Pulido-Villena E, Reche I (2006) Atmospheric inputs of phosphorus and nitrogen to the southwest Mediterranean region: Biogeochemical responses of high mountain lakes. Limnol Oceanogr 51:830-837

Morris DP, Lewis WM (1988) Phytoplankton nutrient limitation in Colorado mountain lakes. Freshwater Biol 20:315-327

Murphy CA, Thompson PL, Vinebrooke RD (2010) Assessing the sensitivity of alpine lakes and ponds to nitrogen deposition in the Canadian Rocky Mountains. Hydrobiologia 648:83-90

Parker BR, Vinebrooke RD, Schindler DW (2008) Recent climate extremes alter alpine lake ecosystems. PNAS 105:12927-12931

Reynolds CS (2006) The ecology of freshwater phytoplankton. New York, NY. Cambridge University Press

Saros JE, Interlandi SJ, Wolfe AP, Ensgtrom DR (2003) Recent changes in the diatom community structure of lakes in the Beartooth Mountain Range, U.S.A. Arct Antract Alp Res 35:18-23

Saros JE, Michel TJ, Interlandi SJ, Wolfe AP (2005) Resource requirements of *Asterionella Formosa* and *Fragilaria crotonensis* in oligotrophic alpine lakes: implications for recent phytoplankton community reorganizations. Can J Fish Aquat Sci 62:1681-1689

Saros JE, Rose KC, Clow DW, Stephens VC, Nurse AB, Arnett HA, Stone JR, Williamson CE, Wolfe AP (2010) Melting alpine glaciers enrich high-elevation lakes with reactive nitrogen. Environ Sci Technol 44:4891-4896

Schindler DW (1987) Detecting ecosystem responses to anthropogenic stress. Can J Fish Aquat Sci 44:6-25

Schindler DW (2012) The dilemma of controlling cultural eutrophication of lakes. Proc R Soc B 279:4322 4333

Slemmons KEH, Rodgers ML, Stone JR, Saros JE (2017) Nitrogen subsidies in glacial meltwaters have altered planktonic diatom communities in lakes of the US Rocky Mountains for at least a century. Hydrobiologia 800:129-144

Sommaruga R (2015) When glaciers and ice sheets melt: consequences for planktonic organisms. J Plankton Res 37:509-518

Sterner RW (1989) The role of grazers in phytoplankton succession. In: U. Sommer (eds) Plankton ecology: succession in plankton communities. Springer-Verlag, Berlin, pp 107- 170

Thies H, Nickus U, Mair V, Tessadri R, Tait D, Thaler B, Psenner R (2007) Unexpected response of high alpine lake waters to climate warming. Environ Sci Technol 41:7424-7429

Vinebrooke RD, Thompson PL, Hobbs W, Luckman BH, Graham MD, Wolfe AP (2010) Glacially mediated impacts of climate warming on alpine lakes of the Canadian Rocky Mountains. Verh Internat Verein Limnol 30:1449-1452

Vinebrooke RD, MacLennan MM, Bartrons M, Zettel JP (2014) Missing effects of anthropogenic nutrient deposition on sentinel alpine ecosystems. Global Change Biol 20:2173-2182

Vitousek PM, Porder S, Houlton BZ, Chadwick OA (2010) Terrestrial phosphorus limitation: mechanisms, implications, and nitrogen-phosphorus interactions. Ecol Appl 20:5-15

Wolfe AP, Baron JS, Cornett RJ (2001) Anthropogenic nitrogen deposition induces rapid ecological changes in alpine lakes of the Colorado Front Range (USA). J Paleolimnol 25:1-7

Complete List of Literature Cited

Adrian R, O'Reilly CM, Zagarese H, Baines SB, Hessen DO, Keller W, Livingstone DM, Sommaruga R, Straile D, Van Donk E, Weyhenmeyer GA, Winder M (2009) Lakes as sentinels of climate change. Limnol Oceanogr 54:2283-2297

Alexander V, Whalen SC, Klingensmith KM (1989) Nitrogen cycling in Arctic lakes and ponds. Hydrobiologia 172:165-172

Allgeier JE, Rosemond AD, Layman CA (2011) The frequency and magnitude of non-additive responses to multiple nutrient enrichment. J Appl Ecol 48:96-101

Bajard M, Etienne D, Qiunsac S, Dambrine E, Sabatier P, Frossard V, Gaillard J, Develle A-L, Poulenard J, Arnaud F, Dorioz J-M (2018) Legacy of early anthropogenic effects on recent lake eutrophication (Lake Bénit, northern French Alps). Anthropocene 24:72-87

Baron JS, Rueth HM, Wolfe AM, Nydick KR, Allstott EJ, Minear JT, Moraska B (2000) Ecosystem responses to nitrogen deposition in the Colorado front ranges. Ecosystems 3:352-368

Baron JS, Driscoll CT, Stoddard JL, Richer EE (2011) Empirical critical loads of atmospheric nitrogen deposition for nutrient enrichment and acidification of sensitive US lakes. BioScience 61: 602-613

Battarbee RW, Kernan M, Rose N (2009) Threatened and stressed mountain lakes of Europe: Assessment and progress. Aquat Ecosyst Health 12:118-128

Bayer TK, Schallenberg M, Burns CW (2016) Contrasting controls on phytoplankton dynamics in low large, pre-alpine lakes imply differential responses to climate change. Hydrobiologia 771:131-150

Beaulieu M, Pick F, Gregory-Eaves I (2013) Nutrients and water temperature are significant predictors of cyanobacterial biomass in a 1147 lakes data set. Limnol Oceangr 58:1736-1746

Bergström A-K (2010) The use of TN:TP and DIN:TP ratios as indicators for phytoplankton nutrient limitation in oligotrophic lakes affected by N deposition. Aquat Sci 72:277-281

Bergström A-K, Blomqvist P, Jansson M (2005) Effects of atmospheric nitrogen deposition on nutrient limitation and phytoplankton biomass in unproductive Swedish lakes. Limnol Oceanogr 50:987-994

Bergström A-K, Jansson M (2006) Atmospheric nitrogen deposition has caused nitrogen enrichment and eutrophication of lakes in the northern hemisphere. Global Change Biol 12:635-643

Bergström A-K, Jonsson A, Jansson M (2008) Phytoplankton responses to nitrogen and phosphorus enrichment in unproductive Swedish lakes along a gradient of atmospheric nitrogen deposition. Aquat Biol 4:55-64

Bergström A-K, Faithful C, Karlsson D, Karlsson J (2013) Nitrogen deposition and warming - effects on phytoplankton nutrient limitation in subarctic lakes. Global Change Biol 19:2557-2568

Billings WD, Mooney HA (1968) The ecology of arctic and alpine plants. Biol Rev 43:481-529

Bird DF, Kalff K (1986) Bacterial grazing by planktonic lake algae. Science 231:493-495

Blais JM, Schindler DW, Muir DCG, Sharp M, Donald D, Lafrieniere M, Braekvelt E, Strachan WMJ (2001) Melting glaciers: A major source of persistent organochlorines to subalpine Bow Lake in Banff National Park, Canada. Ambio 30:410-415

ter Braak CJF, Smilauer P (2012) Canoco Reference Manual and User's Guide: Software for Ordinations (Version 5.0). Microcomputer Power, Ithaca

Bracken MES, Hillbrand H, Borer ET, Seabloom EW, Cebrian J, Cleland EE, Elser JJ, Gruner DS, Harpole WS, Ngai JT, Smith JE (2015) Signatures of nutrient limitation and co-limitation: responses of autotroph internal nutrient concentrations to nitrogen and phosphorus addition. Oikos 124:113-121

Brahney J, Ballentyne AP, Kociolek P, Spaulding S, Out M, Porwoll T, Neff JC (2014) Dust mediated transfer of phosphorus to alpine lake ecosystems of the Wind River Range, Wyoming, USA. Biogeochemistry 120:259-278

Brahney J, Mahowald N, Ward DS, Ballantyne AP, Neff JC (2015) Is atmospheric phosphorus pollution altering global alpine Lake stoichiometry? Global Biogeochem Cycles 29:1369-1383

Bunting L, Leavitt PR, Weidman RP, Vinebrooke RD (2010) Regulation of the nitrogen biogeochemistry of mountain lakes by subsidies of terrestrial dissolved organic matter and the implications for climate studies. Limnol Oceanogr 55:333-345

Cabello-Yeves PJ, Picazo A, Camacho A, Callieri C, Rosselli R, Roda-Garcia JJ, Couthino FH, Rodriguez-Valera F (2018) Ecological and genomic features of two widespread freshwater picocyanobacterial. Environ Microbiol 20:3757-3771

Callieri C (2007) Regulation of the nitrogen biogeochemistry of mountain lakes by subsidies of terrestrial dissolved organic matter and the implications for climate studies. Freshwater Reviews 1:1-28

Callieri C (2017) *Synechococcus* plasticity under environmental change. FEMS Microbiol Lett 364:fnx229

Callieri C, Stockner J (2000) Picocyanobacteria success in oligotrophic lakes: fact of fiction? J Limnol 59:72-76

Camacho A, Miracle MR, Vicente E (2003) Which factors determine the abundance and distribution of picocyanobacterial in inland waters? A comparison among different types of lakes and ponds. Arch Hydrobiol 157:321-338

Camarero L, Rogora M, Mosello R, Anderson NJ, Barbieri A, Botev I, Kernan M, Kopáček J, Korhola A, Lotter AF, Muri G, Postolache C, Stuchlik E, Thies H, Wright RF (2009) Regionalisation of chemical variability in European mountain lakes. Freshwater Biol 54:2452-2469

Camarero L, Catalan J (2012) Atmospheric phosphorus deposition may cause lakes to revert from phosphorus limitation back to nitrogen limitation. Nature Communications 3:1118, DOI: 10.1038/ncomms2125

Campbell H, Baron JS, Tonnessen KA, Brooks PD, Schuster PF (2000) Controls on nitrogen flux in alpine/subalpine watersheds of Colorado. Water Resour Res 36:37-47

Carpenter SR (1996) Microcosm experiments have limited relevance for community and ecosystem ecology. Ecology 77:677-680

Catalan J, Bartrons M, Camarero L, Grimalt (2013) Mountain waters as witnesses of global pollution. In: Pechan P, de Vries GE (eds) Living with water: Targeting quality in a dynamic world. Springer, New York, pp 31-67

Clarke GKC, Jarosch AH, Anslow FS, Radic V, Menounos B (2015) Projected deglaciation of western Canada in the twenty-first century. Nature Geoscience 8:372-377

Clow DW (2010) Changes in the timing of snowmelt and streamflow in Colorado: A response to recent warming. J Clim 23:2293-2306

Clow DW, Sueker JK (2000) Relations between basin characteristics and stream water chemistry in alpine/subalpine basins in Rocky Mountain National Park, Colorado. Water Resour Res 36:49-61

Colombo N, Bocchiola D, Martin M, Confortola G, Salerno F, Godone D, D'Amico ME, Freppaz M (2019) High export of nitrogen and dissolved organic carbon from an alpine glacier (Indren Glaciers, NW Italian Alps). Aquat Sci 81:74

Cooper JT, Sinclair GA, Wawrik B (2016) Transcriptome analysis of Scrippsiella trochoidea CCMP 3099 reveals physiological changes related to nitrate depletion. Frontiers in Micrbiol 7: DOI: 10.3389/fmicb.2016.00639

Cottingham KL, Carpenter SR, St. Amand AL (1988) Responses of epilimnetic phytoplankton to experimental nutrient enrichment in three small seepage lakes. J Plankton Res 20:1889-1914

Crowley KF, McNeil BE, Lovett GM, Canham CD, Driscoll CT, Rustad LE, Denny E, Hallet RA, Arthur MA, Boggs JL, Goodale CL, Kahl JS, McNulty SG, Ollinger SV, Pardo LH, Schaberg PG, Stoddard JL, Weand MP, Weathers KC (2012) Do nutrient limitation patterns shift from nitrogen toward phosphorus with increasing nitrogen deposition across the Northeastern United States. Ecosystems 15:940-957

Daggett CT, Saros JE, Lafrancois BM, Simon KS, Amirbahman A (2015) Effects of increased concentrations of inorganic nitrogen and dissolved organic matter on phytoplankton in boreal lakes with differing nutrient limitations patterns. Aquat Sci 77:511-521

Davidson EA, Howarth RW (2007) Environmental science: nutrients in synergy. Nature 449:1000-1001

Downing JA (2010) Emerging global role of small lakes and ponds: little things mean a lot. Limnetica 29:9-24

Downing JA, McCauley E (1992) The nitrogen: phosphorus relationship in lakes. Limnol Oceanogr 37:936-945

Downing JA, Prairie YT, Cole JJ, Duarte CM, Tranvik LJ, Striegl RG, McDowell WH, Kortelainen P, Caraco NF, Melack JM, Middelburg JJ (2006) The global abundance and size distribution of lakes, ponds, and impoundments. Limnol Oceanogr 51:2388-2397

Ejarque E, Khan S, Steniczka G, Schelker J, Kainz MJ, Battin TJ (2018) Climate-induced hydrological variation controls the transformation of dissolved organic matter in a subalpine lake. Limnol Oceanogr 63:1355-1371

Elser JJ, Marzolf ER, Goldman CR (1990) Phosphorus and nitrogen limitation of phytoplankton growth in the freshwaters of North America: a review and critique of experimental enrichments. Can J Fish Aquat Sci 47:1468-1477

Elser JJ, Bracken MES, Cleland EE, Gruner DS, Harpole WS, Hillebrand H, Ngai JT, Seabloom EW, Shurin JB, Smith JE (2007) Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. Ecol Lett 10:1135-1142

Elser JJ, Anderson T, Baron JS, Bergström A-K, Jansson M, Kyle M, Nydick KR, Steger L, Hessen DO (2009) Shifts in lake N:P stoichiometry and nutrient limitation driven by atmospheric nitrogen deposition. Science 326:835-837

Evans CD, Monteith DT, Cooper DM (2005) Long-term increases in surfaces water dissolved organic carbon: Observations, possible causes and environmental impacts. Environ Pollut 137:55-71

Fenn ME, Baron JS, Allen EB, Rueth HM, Nydick KR, Geiser L, Bowman WD, Sickman JO, Meixner T, Johnson DW, Neitlich P (2003) Ecological effects of nitrogen deposition in the Western United States. BioScience 53:404-420

Fountain AG, Campbell JL, Schuur EAG, Stammerjohn SE, Williams MW, Ducklow HW (2012) The disappearing cryosphere: Impacts and ecosystem responses to rapid cryosphere loss. BioScience 62:405-415

Freeman C, Evans CD, Monteith DT, Reynolds B, Fenner N (2001) Export of organic carbon from peat soils. Nature 412:785

Gallina F, Anneville O, Beniston M (2011) Impacts of extreme air temperatures on cyanobacteria in five deep peri-Alpine lakes. J Limnol 70:186-196

García-Jurado F, de Vicente I, Galotti A, Reul A, Jiménez-Gómez F, Guerrero F (2012) Effects of drought conditions on plankton community and on nutrient availability in an oligotrophic high mountain lake. Arct Antarct Alp Res 44:50-61

Gardner EM, McKnight DM, Lewis WM, Miller MP (2008) Effects of nutrient enrichment on phytoplankton in an alpine lake, Colorado U.S.A. Arct Antarct Alp Res 40:55-64

Gonzales EJ (2000) Nutrient enrichment and zooplankton effects on the phytoplankton community in microcosms from El Andino reservoir (Venezuela). Hydrobiologia 434:81-96

Graham MD, Vinebrooke RD (2009) Extreme weather events alter planktonic communities in boreal lakes. Limnol Oceanogr 54:2481-2492

Harpole WS, Ngai JT, Cleland EE, Seabloom EW, Borer ET, Bracken MES, Elser JJ, Gruner DS, Hillebrand H, Shurin JB, Smith JE (2011) Nutrient co-limitation of primary producer communities. Ecol Lett 14:852-862

Harsch MA, Hulme PE, McGlone MS, Duncan RP (2009) Are treelines advancing? A global meta-analysis of treeline response to climate warming. Ecol Lett 12:1040-1049

Heard AM, Sickman JO (2016) Nitrogen assessment points: development and application to high-elevation lakes in the Sierra Nevada, California. Ecosphere 7(11):e01586

Huss M, Bookhagen B, Huggel C, Jacobsen D, Bradley RS, Clague JJ, Vuille M, Buytaert W, Cayan DR, Greenwood G, Mark BG, Miler AM, Weingartner R, Winder M (2017) Toward mountains without permanent snow and ice. Earth's Future 5:418-435

Jacquemin C, Bertrand C, Oursel B, Thorel M, Franquet E, Cavalli L (2018) Growth rate of alpine phytoplankton assemblages from contrasting watersheds and N-deposition regimes exposed to nitrogen and phosphorus enrichments. Freshwater Biol 63:1326-1339

Jacquemin C, Bertrand C, Franquet E, Mounier S, Misson B, Oursel B, Cavalli L (2019) Effects of catchment area and nutrient deposition regime on phytoplankton functionality in alpine lakes. Sci Total Environ 674:114-127

Jeffrey SW, Mantoura RFC, Wright SW (2005) Phytoplankton pigments in oceanography: guidelines to modern methods, UNESCO, Madrid

Kamenik C, Schmidt R, Kum G, Psenner R (2001) The influence of catchment characteristics on the water chemistry of mountain lakes. Arct Antarct Alp Res 33:404-409

Kissman CEH, Williamson CE, Rose KC, Saros JE (2013) Response of phytoplankton in an alpine lake to inputs of dissolved organic matter through nutrient enrichment and trophic forcing. Limnol Oceanogr 58:867-880

Klug JL (2002) Positive and negative effects of allochthonous dissolved organic matter and inorganic nutrients on phytoplankton growth. Can J Fish Aquat Sci 59:85-95

Kolzau S, Wiedner C, Rucker J, Kohler J, Kohler A, Dolman AM (2014) Seasonal patterns of nitrogen and phosphorus limitation in four German lakes and the predictability of limitation status from ambient nutrient concentrations. PLoS ONE 9:e96065

Kopáček J, Stuchlík E, Straškrabová V, Pšenáková P (2000) Factors governing nutrient status of mountain lakes in the Tatra Mountains. Freshwater Biol 43:369-383

Kopáček J, Kaňa J, Šantrůčková H, Picek T, Stuchlík E (2004) Chemical and biological characteristics of alpine soils in the Tatra mountains and their correlation with lake water quality. Water Air Soil Pollut 153:307-327

Kopáček J, Hejzlar J, Vrba J, Stuchlík E (2011) Phosphorus loading of mountain lakes: Terrestrial export and atmospheric deposition. Limnol Oceanogr 56:1343-1354

Krajewska M, Szymczak-Zyla M, Kobos J, Witak M, Kowalewska G (2019) Canthaxanthin in recent sediments as an indicator of heterocystous cyanobacteria in coastal waters. Oceanologia 61:78-88

Leavitt PR, Schindler DE, Paul AJ, Hardie AK, Schindler DW (1994) Fossil pigment records of phytoplankton in trout-stocked alpine lakes. Can J Fish Aquat Sci 51:2411-2423

Levine MA, Whalen SC (2001) Nutrient limitation of phytoplankton production in Alaskan Arctic foothill lakes. Hydrobiologia 455:189-201

Li X, Ding Y, Xu J, He X, Han T, Kang S, Wu Q, Mika S, Yu Z, Li Q (2018) Importance of mountain glaciers as a source of dissolved organic carbon. J Geophys Res-Earth 123:2123-2134

Loewen CJG, Vinebrooke RD (2016) Regional diversity reverses the negative impacts of an alien predator on local species-poor communities. Ecology 97:2740-2749

Loewen CJG, Strecker AL, Larson GL, Vogel A, Fisher JM, Vinebrooke RD (2019) Macroecological drivers of zooplankton communities across the mountains of western North America. Ecograhpy 42:791-803

Luettich RA, Harleman DRF, Somlyody L (1990) Dynamic behaviour of suspended sediment concentrations in a shallow lake perturbed by episodic wind events. Limnol Oceanogr 35:1050-1067

Maberly SC, King L, Dent MM, Jones RI, Gibson CE (2002) Nutrient limitation of phytoplankton and periphyton growth in upland lakes. Freshwater Biol 47:2136-2152

MacLennan MM, Dings-Avery C, Vinebrooke RD (2015) Invasive trout increase the climatic sensitivity of zooplankton communities in naturally fishless lakes. Freshwater Biol 60:1502-1513

Mahowald N, Jickells TD, Baker AR, Artaxo P, Benitez-Nelson CR, Bergametti G, Bond TC, Chen Y, Cohen DD, Herut B, Kubilay N, Losno R, Luo C, Maenhaut W, McGee KA, Okin GS, Siefert RL, Tsukuda S (2008) Global distribution of atmospheric phosphorus sources, concentrations and deposition rates, and anthropogenic impacts. Global Biogeochem Cycles 22:GB4026

Marchetto A, Rogora M, Boggero A, Musazzi S, Lami A, Lotter AF, Tolotti M, Thies H, Psenner R, Massaferro J, Barbieri A (2009) Response of alpine lakes to major environmental gradients, as detected through planktonic, benthic and sedimentary assemblages. Advanc Limnol 62:389-410

Martin C, Frenette J-J, Morin J (2005) Changes in the spectral and chemical properties of a water mass passing through extensive macrophyte beds in a large fluvial lake (Lake Saint-Pierre, Québec, Canada). Aquat Sci 67:196-209

McCormick PV, Cairns J (1994) Algae as indicators of environmental change. J Appl Phycol 6:509-526

McKnight DM, Andrews ED, Spaulding SA, Aiken GR (1994) Aquatic fulvic acids in algal-rich Antarctic ponds. Limnol Oceanogr 39:1972-1979

McKnight DM, Harnish R, Wernshaw RL, Baron JS, Schiff SS (1997) Chemical characteristics of particulate, colloidal, and dissolved organic material in Loch Vale watershed, Rocky Mountain National Park. Biogeochemistry 36:99-124

McMaster, NL (2003) The effects of climate change and nitrogen deposition on the limnology of alpine ponds. Master's thesis, University of Alberta, Edmonton

McMaster NL, Schindler DW (2005) Planktonic and epipelic algal communities and their relationship to physical and chemical variables in alpine ponds in Banff National Park, Canada. Arct Antarct Alp Res 37:337-347

McNaught AS, Schindler DW, Parker BM, Paul AJ, Anderson RS, Donald DB, Agbeti M (1999) The restoration of an alpine lake food web following fish stocking. Limnol Oceanogr 44:127-136

Medina-Sánchez JM, Villar-Argaiz M, Carrillo P (2004) Neither with nor without you: a complex algal control on bacterioplankton in a high mountain lake. Limnol Oceanogr 49:1722-1733

Mladenov N, Williams MW, Schmidt SK, Cawley K (2012) Atmospheric deposition as a source of carbon and nutrients to an alpine catchment of the Colorado Rocky Mountains. Biogeosciences 9:3337-3355

Morales-Baquero R, Pulido-Villena E, Reche I (2006) Atmospheric inputs of phosphorus and nitrogen to the southwest Mediterranean region: Biogeochemical responses of high mountain lakes. Limnol Oceanogr 51:830-837

Morris DP, Zagarese H, Williamson CE, Balseiro EG, Hargreaves BR, Modenutti B, Moeller R, Quimalinos C (1995) The attenuation of solar UV radiation in lakes and the role of dissolved organic carbon. Limnol Oceanogr 40:1381-1391

Morris DP, Lewis WM (1988) Phytoplankton nutrient limitation in Colorado mountain lakes. Freshwater Biol 20:315-327

Moser KA, Baron JS, Brahney J, Oleksy IA, Saros JE, Hundley EJ, Sadro SA, Kopáček J, Sommarua R, Kainz MJ, Strecker AL, Chandra S, Walters DM, Preston DL, Michelutti N, Lepori F, Spaulding SA, Christianson KR, Melack JM, Smol JP (2019) Mountain lakes: Eyes on global environmental change. Glob Planet Change 178:77-95

Müller S, Mitrovic SM (2015) Phytoplankton co-limitation by nitrogen and phosphorus in a shallow reservoir: progression from the phosphorus limitation paradigm. Hydrobiologia 744:255-269

Murphy CA, Thompson PL, Vinebrooke RD (2010) Assessing the sensitivity of alpine lakes and ponds to nitrogen deposition in the Canadian Rocky Mountains. Hydrobiologia 648:83-90

Nanus L, Clow DW, Saros JE, Stephens VC, Campbell DH (2012) Mapping critical loads of nitrogen deposition for aquatic ecosystems in the Rocky Mountains, USA. Environ Pollut 166:125-135

Nydick KR, Lafrancois BM, Baron JS, Johnson BM (2003) Lake-specific responses to elevated atmospheric nitrogen deposition in the Colorado Rocky Mountains, U.S.A. Hydrobiologia 510:103-114

O'Donnell DR, Wilburn P, Silow EA, Yampolsky LY, Litchman E (2017) Nitrogen and phosphorus colimitation of phytoplankton in Lake Baikal: insights from a spatial survey and nutrient enrichment experiments. Limnol Oceanogr 62:1383-1392

Ogbebo FE, Evans MS, Waiser MJ, Tumber VP, Keating JJ (2009) Nutrient limitation of phytoplankton growth in Arctic lakes of the lower Mackenzie River Basin, northern Canada. Can J Fish Aquat Sci 66:247-260

Orihel DM, Schindler DW, Ballard NC, Graham MD, O'Connell DW, Wilson LR, Vinebrooke RD (2015) The "nutrient pump:" Iron-poor sediments fuel low nitrogen-to-phosphorus ratios and cyanobacterial blooms in polymictic lakes. Limnol Oceanogr 60:856-871

O'Neil JM, Davis TW, Burford MA, Gobler CJ (2012) The rise of harmful cyanobacteria blooms: The potential roles pf eutrophication and climate change. Harmful Algae 14:313-334

Pardo LH, Fenn ME, Goodale CL, Geiser LH, Driscoll CT, Allen EB, Baron JS, Bobbink R, Bowman WD, Clark CM, Emmett B, Gilliams FS, Greaver TL, Hall SJ, Lilleskov EA, Liu L, Lynch JA, Nadelhoffer KJ, Perakis SS, Robin-Abbott MJ, Stoddard JL, Weathers KC, Dennis RL (2011) Effects of nitrogen deposition and empirical nitrogen critical loads for ecoregions of the United States. Ecol Appl 21:3049-3082

Paerl HW, Paul VJ (2012) Climate change: Links to global expansion of harmful cyanobacteria. Water Research 46:1349-1363

Palazzi E, Mortarini L, Terzago S, von Hardenberg J (2019) Elevation‑dependent warming in global climate model simulations at high spatial resolution. Clim Dyn 52:2685-2702

Parker BR, Vinebrooke RD, Schindler DW (2008) Recent climate extremes alter alpine lake ecosystems. PNAS 105:12927-12931

Parmar TK, Rawtani D, Agrawal YK (2016) Bioindicators: the natural indicator of environmental pollution. Bioindicators 9:110-118

Pepin N, Bradley RS, Diaz HF, Baraer M, Caceres ED, Forsythe N, Fowler H, Greenwood G, Hashmi MZ, Liu XD, Miller JR, Ning L, Ohmura A, Palazzi E, Rangwala I, Schöner W, Severskiy I, Shahgedanova M, Wang MB, Williamson SN, Yang D (2015) Elevation-dependent warming in mountain regions of the world. Nat Clim Change 5:424–430

Pienitz R, Vincent WF (2000) Effect of climate change relative to ozone depletion on UV exposure in subarctic lakes. Nature 404:484-487

Porcel S, Saad FJ, Sabio Y Garcia CA, Izaguirre I (2019) Microbial planktonic communities in lakes from a Patagonian basaltic plateau: influence of the water level decrease. Aquat Sci 81:51

Preston DL, Caine N, McKnight DM, Williams MW, Hell K, Miller MP, Hart SJ, Johnson PTJ (2016) Climate regulates alpine lake ice cover phenology and aquatic ecosystem structure. Geophys Res Lett 43:5353-5360

Przytulska A, Bartosiewicz M, Vincent WF (2017) Increased risk of cyanobacterial blooms in northern high-latitude lakes through climate warming and phosphorus enrichment. Freshwater Biol 62:1986-1996

Reynolds CS (2006) The ecology of freshwater phytoplankton. New York, NY. Cambridge University Press

Roberts JJ, Fausch KD, Schmidt TS, Walters DM (2017) Thermal regimes of Rocky Mountain lakes warm with climate change. PLoS ONE 12: e0179498

Rothhaupt KO (1996) Laboratory experiments with a mixotrophic chrysophyte and obligately phagotrophic and phototrophic competitors. Ecology 77:716–724

Ruber J, Bauer FR, Millard AD, Raeder U, Geist J, Zwirglmaier K (2016) *Synechococcus* diversity along a trophic gradient in the Osterseen Lake District, Bavaria. Microbiology 162:2053-2063

Sadro S, Nelson CE, Melack JM (2012) The influence of landscape position and catchment characteristics on aquatic biogeochemistry in high-elevation lake-chains. Ecosystems 15:363-386

Sadro S, Sickman JO, Melack JM, Skeen K (2018) Effects of climate variability on snowmelt and implications for organic matter in a high-elevation lake. Water Resour Res 54:4563-4578

Sanders RW, Cooke SL, Fisher JM, Fey SB, Heinze AW, Jeffrey WH, Macaluso AL, Moeller RE, Morris DP, Neale PJ, Olson MH, Pakulski DJ, Porter JA, Schoener DM, Williamson CE (2015) Shifts in microbial food web structure and productivity after additions of naturally occurring dissolved organic matter: Results from large-scale lacustrine mesocosms. Limnol Oceanogr 60:2130-2144

Sandgren CD (1988) The ecology of chrysophytes flagellates: Their growth and perennation strategies as freshwater phytoplankton. Cambridge, Cambridge University Press.

Saros JE, Interlandi SJ, Wolfe AP, Ensgtrom DR (2003) Recent changes in the diatom community structure of lakes in the Beartooth Mountain Range, U.S.A. Arct Antract Alp Res 35:18-23

Saros JE, Michel TJ, Interlandi SJ, Wolfe AP (2005) Resource requirements of *Asterionella Formosa* and *Fragilaria crotonensis* in oligotrophic alpine lakes: implications for recent phytoplankton community reorganizations. Can J Fish Aquat Sci 62:1681-1689

Saros JE, Rose KC, Clow DW, Stephens VC, Nurse AB, Arnett HA, Stone JR, Williamson CE, Wolfe AP (2010) Melting alpine glaciers enrich high-elevation lakes with reactive nitrogen. Environ Sci Technol 44:4891-4896

Schiaffino MR, Unrein F, Gasol JM, Massan R, Balague V, Izaguirre I (2011) Bacterial community structure in a latitudinal gradient of lakes: the role of spatial versus environmental factors. Freshwater Biol 56:1973-1991

Schindler DW (1974) Eutrophication and recovery in experimental lakes: implications for lake management. Science 184:897-899

Schindler DW (1977) Evolution of phosphorus limitation in lakes. Science 195:260-262

Schindler DW (1987) Detecting ecosystem responses to anthropogenic stress. Can J Fish Aquat Sci 44:6-25

Schindler DW (2000) Aquatic problems caused by human activities in Banff National Park, Alberta, Canada. Ambio 29:401-407

Schindler DW (2012) The dilemma of controlling cultural eutrophication of lakes. Proc R Soc B 279:4322-4333

Schindler DE, Knapp RA, Leavitt PR (2001) Alteration of nutrient cycles and algal production resulting from fish introductions into mountain lakes. Ecosystems 4:308–321

Schindler DW Parker BR (2002) Biological pollutants: Alien fished in mountain lakes. Water Air Soil Pollut 2:379-397

Schindler DW, Dillon PJ, Schreier H (2006) A review of anthropogenic sources of nitrogen and their effects on Canadian aquatic ecosystems. Biogeochemistry 79:25-44

Sickman JO, Melack JM, Clow DW (2003) Evidence for nutrient enrichment of high-elevation lakes in the Sierra Nevada, California. Limnol Oceanogr 48:1885-1892

Slemmons KEH, Saros JE (2012) Implications of nitrogen-rich glacial meltwater for phytoplankton diversity and productivity in alpine lakes. Limnol Oceanogr 57:1651-1663

Slemmons KEH, Saros JE, Simon K (2013) The influence of glacial meltwater on alpine aquatic ecosystems: a review. Environ Sci Processes Impacts 15:1794-1806

Slemmons KEH, Rodgers ML, Stone JR, Saros JE (2017) Nitrogen subsidies in glacial meltwaters have altered planktonic diatom communities in lakes of the US Rocky Mountains for at least a century. Hydrobiologia 800:129-144

Śliwińska-Wilczewska S, Maculewicz J, Felpeto AB, Latala A (2018) Allelopathic and bloom-forming picocyanobacteria in a changing world. Toxins 10:48

Sommaruga R (2015) When glaciers and ice sheets melt: consequences for planktonic organisms. J Plankton Res 37:509-518

Sommaruga R, Augustin G (2006) Seasonality in UV transparency of an alpine lake is associated to changes in phytoplankton biomass. Aquat Sci 68:129-141

Sommer U (1984) The paradox of the plankton – Fluctuations of phosphorus availability maintain diversity of phytoplankton in flow-through cultures. Limnol Oceanogr 29: 633-636

Sterner RW (1989) The role of grazers in phytoplankton succession. In: U. Sommer (eds) Plankton ecology: succession in plankton communities. Springer-Verlag, Berlin, pp 107- 170

Stomp M, Huisman J, Mittelbach GG, Litchman E, Klausmeier CA (2011) Large-scale biodiversity patterns in freshwater phytoplankton. Ecology 92:2096-2107

Symons CC, Arnott SE, Sweetman JN (2012) Nutrient limitation of phytoplankton communities in Subarctic lakes and ponds in Wapusk National Park, Canada. Polar Biol 35:481-489

Taranu ZE, Grergory-Eaves I, Leavitt PR, Bunting L, Buchaca T, Catalan J, Domaison I, Guilizzoni P, Lami A, McGowan S, Moorhouse H, Morabito G, Frances FR, Stevensen MA, Thompson PL, Vinebrooke RD (2015) Acceleration of cyanobacterial dominance in north temperate-subarctic lakes during the Anthropocene. Ecol Lett 18:375-384

Teufel AG, Li W, Kiss AJ, Morgan-Kiss, RM (2017) Impact of nitrogen and phosphorus on phytoplankton production and bacterial community structure in two stratified Antarctic lakes: a bioassay approach. Polar Biol 40: 1007-1022

Thies H, Nickus U, Mair V, Tessadri R, Tait D, Thaler B, Psenner R (2007) Unexpected response of high alpine lake waters to climate warming. Environ Sci Technol 41:7424-7429

Thompson R, Kamenik C, Schmidt R (2005) Ultra-sensitive alpine lakes and climate change. J Limnol 63:139-152

Tilman D, Kiesling R, Sterner R, Kilham SS, Johnson FA (1986) Green, bluegreen and diatom algae: taxonomic differences in competitive ability for phosphorus, silicon and nitrogen. Arch Hydrobiol 106:473-485

Tolotti M, Thies H, Cantonati M, Hansen CME, Thaler B (2003) Flagellate algae (Chrysophyceae, Dinophyceae, Cryptophyceae) in 48 high mountain lakes of the Northern and Southern slope of the Eastern Alps: biodiversity, taxa distribution and their driving variables. Hydrobiologia 502:331-348

Tolotti M, Manca M, Angeli N, Morabito G, Thaler B, Rott E, Stuchlik E (2006) Phytoplankton and zooplankton associations in a set of alpine high altitude lakes: geographic distribution and ecology. Hydrobiologia 562:99-122

Vähätalo AV, Salonen K, Münster U, Järvinen M, Wetzel RG (2003) Photochemical transformation of allochthonous organic matter provides bioavailable nutrients in a humic lake. Arch Hydrobiol 156:287-314

Vanni MJ (2002) Nutrient cycling by animals in freshwater ecosystems. Annu Rev Ecol Syst 33:341-370

Vinebrooke RD, Leavitt PR (1998) Direct and indirect effects of allochthonous dissolved organic matter, inorganic nutrients, and ultraviolet radiation on an alpine littoral food web. Limnol Oceanogr 43:1065-1081

Vinebrooke RD, Leavitt PR (1999a) Phytobenthos and phytoplankton as potential indicators of climate change in mountain lakes and ponds: a HPLC-based pigment approach. J N Am Benthol Soc 18:15-33

Vinebrooke RD, Leavitt PR (1999b) Differential responses of littoral communities to ultraviolet radiation in an alpine lake. Ecology 80:223-237

Vinebrooke RD, Leavitt PR (2005) Mountain lakes as indicators of the cumulative impacts of ultraviolet radiation and other environmental stressors. In: Huber UM, Bugmann HKM, Reasoner MA (eds) Global change and mountain regions: An overview of current knowledge. Springer, Dordrecht, Netherlands, pp 437-447

Vinebrooke RD, Thompson PL, Hobbs W, Luckman BH, Graham MD, Wolfe AP (2010) Glacially mediated impacts of climate warming on alpine lakes of the Canadian Rocky Mountains. Verh Internat Verein Limnol 30:1449-1452

Vinebrooke RD, MacLennan MM, Bartrons M, Zettel JP (2014) Missing effects of anthropogenic nutrient deposition on sentinel alpine ecosystems. Global Change Biol 20:2173-2182

Vitousek PM, Aber JD, Howarth RW, Likens GE, Matson PA, Schindler DW, Schlesinger WH, Tilman DG (1997) Human alteration of the global nitrogen cycle: sources and consequences. Ecol Appl 7:737-750

Vitousek PM, Porder S, Houlton BZ, Chadwick OA (2010) Terrestrial phosphorus limitation: mechanisms, implications, and nitrogen-phosphorus interactions. Ecol Appl 20:5-15

Viviroli D, Durr HH, Messerli B, Meybeck M, Weingartner R (2007) Mountains of the world, water towers for humanity: Typology, mapping, and global significance. Water Resour Res 43:W07447

Vörös L, Callieri C, Balogh KV, Bertoni R (1998) Freshwater picocyanobacterial along a trophic gradient and light quality range. Hydrobiologia 369/370:117-125

Wang Q, Fan X, Wang M (2014) Recent warming amplification over high elevation regions across the globe. Clim Dyn 43:87-101

Wang X, Thompson DK, Marshall GA, Tymstra C, Carr R, Flannigan MD (2015) Increasing frequency of extreme fire weather in Canada with climate change. Clim Change 130:573-586

Wang X, Parisien M-A, Taylor SW, Candau J-N, Stralberg D, Marshall GA, Little JM, Flannigan MD (2017) Projected changes in daily fire spread across Canada over the next century. Environ Res Lett 12:025005

Warner KA, Saros JE, Simon KS (2017) Nitrogen subsidies in glacial meltwater: implications of high elevation aquatic chains. Water Resour Res 53:9791-9806

Waters, MN, Metz AP, Smoak JM, Turner H (2019) Chronic prescribed burning alters nutrient deposition and sediment stoichiometry in a lake ecosystem. Ambio 48:672-682

Watson SB, McCauley E, Downing JA (1997) Patterns in phytoplankton taxonomic composition across temperate lakes of differing nutrient status. Limnol Ocreanogr 42:487-495

Watson SB, Kling H (2017) Lake of the Woods phyto- and picoplankton: spatiotemporal patterns in blooms, community composition, and nutrient status. Lake Reserv Manage 33:415-432

Weidman PR, Schindler DW, Thompson PL, Vinebrooke RD (2014) Interactive effects of higher temperature and dissolved organic carbon on planktonic communities in fishless mountain lakes. Freshwater Biol 59:889-904

Wetzel RG, Likens G (2000) Limnological analysis. Springer-Verlag, New York

Weyhenmeyer GA, Willen E, Sonesten L (2004) Effects of an extreme precipitation event on water chemistry and phytoplankton in the Swedish Lake Mälaren. Boreal Environ Res 9:409-420

Weyhenmeyer GA, Müller RA, Norman M, Tranvik LJ (2016) Sensitivity of freshwater to browning in response to future climate change. Clim Change 134:225-239

Williams JJ, Beutel M, Nurse A, Moore B, Hampton SE, Saros JE (2016) Phytoplankton responses to nitrogen enrichment in Pacific Northwest, USA mountain lakes. Hydrobiologia 776:261-276

Williams JJ, Lynch JA, Saros JE, Labou SG (2017) Critical loads of atmospheric N deposition for phytoplankton nutrient limitation shifts in the western U.S. mountain lakes. Ecosphere 8:e01955

Williamson CE, Dodds W, Kratz TK, Palmer MA (2008) Lakes and streams as sentinels of environmental change in terrestrial and atmospheric processes. Front Ecol Environ 6:247-254

Williamson CE, Saros JE, Schindler DW (2009) Sentinels of change. Science 323:887-888

Wolfe AP, Baron JS, Cornett RJ (2001) Anthropogenic nitrogen deposition induces rapid ecological changes in alpine lakes of the Colorado Front Range (USA). J Paleolimnol 25:1-7

Wolfe AP, Van Gorp AC, Baron JS (2003) Recent ecological and biogeochemical changes in alpine lakes of Rocky Mountain National Park (Colorado, USA): a response to anthropogenic nitrogen deposition. Geobiology 1:153-168

Woodwell GM (2004) Mountains: Top down. Ambio Special Report 13:35-38

Zhang Q, Carroll JJ, Dixon AJ, Anastasio C (2002) Aircraft measurements of nitrogen and phosphorus in and around the Lake Tahoe basin: Implications for possible sources of atmospheric pollutants to Lake Tahoe. Environ Sci Technol 36:4981-4989

Zhang Z, Goldstein HL, Reynolds RL, Hu Y, Wang X, Zhu M (2018) Phosphorus speciation and solubility in aeolian dust deposition in the interior American West. Envrion Sci Technol 52:2658-2667

Zwirglmaier K, Heywood JL, Chamberlain K, Woodward EM, Zubkov MV, Scanlan DJ (2007) Basin-scale distribution patterns of picocyanobacterial lineages in the Atlantic Ocean. Environ Microbiol 9:1278-1290

Appendix A: Supplemental Information for Chapter 3

Table A-3.1 Environmental, physical and chemical variables from surveyed lakes and ponds in Banff National Park (n=27)

Lake	Year	Julian Date	Elevation (m asl)	Annual mean air temperature (˚C)	Annual mean precipitation (mm)	Mean solar radiation (WH m-2)	Lake area (ha)	Catchment area (ha)	Catchment area/lake area
Agnes	2018	227	2118	-2.30	684.57	920617.53	52.29	1774.63	33.93
Baker	2017	221	2207	-2.92	662.16	927292.75	32.08	851.23	26.53
Boom	2017	201	1893	-1.69	675.04	894234.59	86.09	1705.56	19.81
Copper	2017	202	1434	1.00	567.11	834672.55	1.25	63.78	50.97
Eiffel	2017	186	2281	-3.00	694.56	929969.67	7.25	421.75	58.19
Grizzly	2018	234	2170	-2.49	658.43	920269.86	38.06	5632.87	148.01
Herbert	2017	172	1600	0.097	619.81	857342.49	5.29	108.77	20.56
Island	2017	209	1570	0.34	622.62	859313.89	14.72	307.70	20.90
Kingfisher	2017	209	1539	0.23	605.25	859786.35	1.45	49.53	34.14
Laryx	2018	234	2189	-2.20	654.84	922218.55	76.90	877.68	11.41
Lost	2017	194	1692	-0.39	640.75	860701.87	4.39	41.38	9.43
Louise	2017	180	1731	-0.63	681.62	872122.04	75.85	2582.49	34.05
Moraine	2017	180	1887	-1.03	684.72	884494.67	39.04	2665.62	68.29
Mud	2017	172	1600	0.00	614.00	863554.61	5.88	27.50	4.68
Mummy	2018	198	2230	-2.36	669.96	925330.41	163.22	1686.89	10.33
O'Brien	2017	210	2118	-2.40	677.85	919660.67	4.71	196.25	41.69
Pilot	2017	202	1408	1.10	543.00	839942.28	3.04	14.56	4.79
Pharaoh	2018	198	2110	-2.19	661.59	911593.42	81.72	861.80	10.55
Ptarmigan	2017	222	2332	-3.23	665.23	940206.09	25.88	138.01	5.33
Redoubt	2017	221	2393	-3.85	671.14	924256.56	17.38	74.17	4.27
Rockbound	2018	220	2202	-3.04	662.49	924398.04	265.04	5271.62	19.89
Rock Isle	2018	234	2251	-2.49	657.38	929256.53	61.82	2822.84	45.66
Sentinel	2018	221	2423	-3.60	688.23	871634.19	14.69	82.76	5.63
Smith	2017	202	1560	0.06	593.67	839833.36	3.71	34.16	9.22
Taylor	2017	210	2057	-2.54	674.19	911793.68	25.69	313.80	12.22
Temple	2017	186	2179	-3.03	682.30	928975.06	3.11	77.78	25.03
Waterfowl	2017	180	1670	-0.61	684.33	856559.75	71.22	20295.69	284.97

Table A-3.1 (continued)

Lake	Vegetataion cover (%)	Barren land (%)	Catchment slope (˚)	Mixed sedimentary rock (%)	Non-carbonate sedimentary rock (%)	Carbonate sedimentary rock (%)	Maximum depth (m)	Secchi depth (m)	Surface water temperature (˚C)
Agnes	97.43	0.12	6.33	100.00	0.00	0.00	20.5	7.0	12.2
Baker	92.90	2.90	12.43	100.00	0.00	0.00	12.4	12.4	15.8
Boom	95.17	0.00	1.69	100.00	0.00	0.00	13.2	10.0	15.0
Copper	55.30	0.98	13.85	36.41	63.59	0.00	10.4	8.5	15.9
Eiffel	93.83	1.20	9.31	100.00	0.00	0.00	13.3	11.7	9.6
Grizzly	31.85	33.05	30.73	96.82	3.05	0.13	3.0	2.0	12.8
Herbert	42.11	44.82	25.02	98.45	1.11	0.44	12.8	6.5	14.1
Island	88.51	0.00	2.51	100.00	0.00	0.00	6.4	4.5	17.3
Kingfisher	9.81	90.19	23.87	78.15	0.08	21.77	6.7	5.0	17.2
Laryx	38.36	59.72	30.52	100.00	0.00	0.00	10	8.0	14.0
Lost	84.04	1.88	1.38	100.00	0.00	0.00	5.5	2.3	18.5
Louise	50.70	49.30	30.90	100.00	0.00	0.00	70.1	0.5	9.5
Moraine	39.33	60.61	17.56	100.00	0.00	0.00	22.8	5.0	6.9
Mud	30.72	68.30	24.27	100.00	0.00	0.00	6.9	3.0	14.1
Mummy	8.41	90.59	18.33	100.00	0.00	0.00	24.0	9.0	10.5
O'Brien	85.24	12.96	10.60	71.23	0.48	28.28	20.6	5.0	6.3
Pilot	44.55	55.45	31.62	100.00	0.00	0.00	8.0	6.0	15.5
Pharaoh	99.41	0.59	11.21	100.00	0.00	0.00	18.0	7.5	13.5
Ptarmigan	52.81	45.37	28.46	100.00	0.00	0.00	22.0	10.5	14.5
Redoubt	48.86	49.13	30.82	100.00	0.00	0.00	10.6	8.5	14.3
Rockbound	42.16	36.62	22.00	99.50	0.21	0.29	16.0	10.0	13.8
Rock Isle	97.43	0.12	6.33	100.00	0.00	0.00	12.5	8.5	14.1
Sentinel	92.90	2.90	12.43	100.00	0.00	0.00	6.7	6.0	12.5
Smith	95.17	0.00	1.69	100.00	0.00	0.00	9.7	2.5	10.8
Taylor	55.30	0.98	13.85	36.41	63.59	0.00	43.9	4.0	9.6
Temple	93.83	1.20	9.31	100.00	0.00	0.00	14.0	6.5	3.1
Waterfowl	31.85	33.05	30.73	96.82	3.05	0.13	4.7	0.5	9.7

Table A-3.1 (continued)

Lake	Conductivity (µS^{-cm})	TN:TP (mass)	TP (µg L^{-1})	TDP (µg L^{-1})	TN (µg L^{-1})	TDN (µg L^{-1})	DOC (mg L^{-1})	pH	Surface dissolved oxygen (%)	Fish (presence /absence)
Agnes	151.1	12.33	9	8	111	78	1.2	7.90	84.1	1
Baker	133.9	9.11	9	1	82	64	1.0	8.46	90.3	1
Boom	174.4	14.25	4	1	57	75	1.1	9.39	82.2	1
Copper	158.0	90.20	10	2	902	878	10.6	8.49	98.2	1
Eiffel	83.3	2.61	36	32	94	107	1.2	8.19	78.0	0
Grizzly	202.9	37.33	9	6	336	319	3.1	8.40	100.8	1
Herbert	337.2	96.00	4	1	384	406	4.2	8.12	84.9	1
Island	198.9	102.00	6	4	612	568	9.6	8.69	99.2	0
Kingfisher	209.9	21.14	35	27	740	740	10.4	8.51	102.6	1
Laryx	163.5	16.64	11	7	183	168	2.2	8.20	84.5	1
Lost	205.8	50.75	4	2	203	201	3.3	9.30	90.4	1
Louise	174.7	19.71	7	5	138	178	1.0	8.51	86.6	1
Moraine	173.4	51.33	3	1	154	153	0.2	8.27	86.5	1
Mud	231.2	57.80	5	2	289	299	7.4	8.30	84.6	1
Mummy	383.7	17.75	4	3	71	60	0.5	9.10	79.9	1
O'Brien	63.9	19.33	3	9	58	103	2.3	8.11	87.2	1
Pilot	326.9	76.50	20	8	1530	1520	7.2	8.23	98.3	1
Pharaoh	89.8	5.4375	16	13	87	78	1.0	8.66	82.4	1
Ptarmigan	70.9	4.82	34	29	164	74	1.3	8.75	86.8	1
Redoubt	108.1	14.20	5	1	71	90	0.6	7.79	87.0	1
Rockbound	150.2	8.33	12	5	100	74	0.8	8.27	83.3	1
Rock Isle	159.6	23.75	8	4	190	164	1.5	8.30	80.1	1
Sentinel	145.6	22.40	5	4	112	83	0.4	9.15	82.4	0
Smith	264.5	6.625	16	13	106	112	2.9	8.02	86.3	1
Taylor	65.1	9.75	4	4	39	59	0.8	7.66	87.7	1
Temple	107.5	12.33	12	2	148	95	0.4	7.88	74.8	1
Waterfowl	197.2	94.00	1	1	94	107	0.2	8.39	83.9	1

Abbreviations are total phosphorus (TP), total dissolved phosphorus (TDP), total nitrogen (TN), total dissolved nitrogen (TDN), dissolved organic carbon (DOC). In cases where concentrations were below detection limits, the detection limit was reported.

Table A-3.2 Environmental, physical and chemical variables from surveyed lakes and ponds in Jasper National Park (n=25)

Lake	Year	Julian Date	Elevation (m asl)	Annual mean air temperature (˚C)	Annual mean precipitation (mm)	Mean solar radiation (WH m^{-2})	Lake area (ha)	Catchment area (ha)	Catchment area/lake area
Annette	2017	205	1024	2.90	468.95	771269.19	27.15	152.34	5.61
Beauvert	2017	205	1030	2.85	490.68	773555.13	35.19	409.95	11.65
Buck	2017	206	1405	0.79	535.00	815806.11	20.87	56.18	2.69
Cabin	2017	208	1217	1.93	592.72	793645.15	34.86	1934.37	55.48
Caledonia	2017	208	1161	2.07	555.19	790266.36	15.16	922.65	60.84
Celestine	2017	212	1260	1.54	520.32	796146.61	40.93	328.79	8.03
Christine	2017	207	1338	1.50	548.00	814940.41	1.11	12.40	11.14
Cutt	2017	215	1455	0.72	585.67	810125.63	5.99	27.46	4.59
Dorothy	2017	207	1336	1.35	554.11	809746.79	25.55	207.25	8.11
Edith	2017	207	1024	2.90	469.63	772760.67	53.91	117.36	2.18
Golden	2017	215	1485	0.75	585.03	804641.79	5.07	13.60	2.68
Honeymoon	2017	206	1405	0.80	534.21	814869.24	17.02	58.77	3.45
Horseshoe	2017	206	1230	1.00	547.63	799502.23	8.04	93.95	11.68
Iris	2017	207	1302	1.42	552.47	805955.02	5.37	254.20	47.34
J436	2017	215	1455	0.80	584.33	822592.44	7.65	35.62	4.66
Leach	2017	206	1237	1.60	521.97	797943.99	8.04	135.39	16.85
Little Honeymoon	2017	206	1310	1.00	534.24	811752.41	0.81	68.58	84.50
Marjorie	2017	208	1143	2.15	516.98	782772.40	9.48	251.73	26.55
16 ½ Mile	2017	206	1174	1.72	517.22	794550.94	7.69	57.13	7.43
Mina	2017	208	1214	2.05	505.24	794055.68	9.23	35.62	3.86
Moab	2017	206	1204	1.55	583.25	796771.94	21.34	487.71	22.85
Osprey	2017	206	1387	0.75	581.19	810528.30	4.90	428.17	87.47
Patricia	2017	205	1180	2.20	498.65	790551.25	64.53	251.48	3.90
Pyramid	2017	205	1186	2.15	553.40	790205.18	124.19	2958.50	23.82
Virl	2017	207	1305	1.60	543.12	809473.62	3.71	42.70	11.51

Table A-3.2 (continued)

Lake	**Vegetataion cover (%)**	**Barren land (%)**	**Catchment slope (˚)**	**Mixed sedimentary rock (%)**	**Non-carbonate sedimentary rock (%)**	**Carbonate sedimentary rock (%)**	**Maximum depth (m)**	**Secchi depth (m)**	**Surface water temperature (˚C)**
Annette	72.92	1.25	3.86	100.00	0.00	0.00	22.8	10.5	16.8
Beauvert	74.65	1.28	6.88	100.00	0.00	0.00	24.8	12.0	14.9
Buck	59.23	0.00	2.23	100.00	0.00	0.00	6.2	6.0	18.1
Cabin	83.00	12.87	14.85	100.00	0.00	0.00	27.0	5.5	17.1
Caledonia	92.99	0.43	9.93	100.00	0.00	0.00	11.3	4.0	17.3
Celestine	85.11	0.83	12.98	29.72	70.28	0.00	13.4	5.5	18.4
Christine	85.57	0.00	11.43	100.00	0.00	0.00	9.2	3.0	16.6
Cutt	53.19	0.00	5.76	100.00	0.00	0.00	8.0	5.5	18.1
Dorothy	78.88	0.73	10.54	100.00	0.00	0.00	14.8	4.0	17.0
Edith	44.20	0.05	2.14	100.00	0.00	0.00	17.3	11.5	18.2
Golden	56.31	0.00	6.47	100.00	0.00	0.00	10.6	8.0	17.6
Honeymoon	70.83	0.00	0.18	100.00	0.00	0.00	7.4	4.0	15.6
Horseshoe	66.47	21.35	23.88	100.00	0.00	0.00	28.6	14.0	16.2
Iris	78.94	0.75	9.56	100.00	0.00	0.00	14.5	4.5	17.1
J436	75.84	0.71	3.87	100.00	0.00	0.00	2.8	2.8	18.5
Leach	83.08	0.61	4.36	100.00	0.00	0.00	11.0	5.5	16.9
Little Honeymoon	71.49	0.65	0.25	100.00	0.00	0.00	5.0	5.0	15.2
Marjorie	89.80	0.38	9.18	100.00	0.00	0.00	8.2	5.5	18.5
16 ½ Mile	83.50	0.00	11.16	100.00	0.00	0.00	5.8	5.8	17.5
Mina	72.29	0.00	5.82	100.00	0.00	0.00	13.8	5.5	19.0
Moab	50.55	39.71	16.77	100.00	0.00	0.00	18.1	9.0	16.1
Osprey	73.37	24.04	20.08	100.00	0.00	0.00	7.5	2.5	8.1
Patricia	67.61	0.33	5.45	100.00	0.00	0.00	41.2	6.9	16.4
Pyramid	80.38	13.53	15.51	100.00	0.00	0.00	18.2	7.0	15.6
Virl	91.11	0.00	7.23	100.00	0.00	0.00	5.8	2.2	19.6

Table A-3.2 (continued)

Lake	Conductivity (μS^{-cm})	TN:TP (mass)	TP (μg L^{-1})	TDP (μg L^{-1})	TN (μg L^{-1})	TDN (μg L^{-1})	DOC (mg L^{-1})	pH	Surface dissolved oxygen (%)	Fish (presence/ absence)
Annette	291.1	24.33	9	2	219	176	0.9	9.43	95.6	1
Beauvert	251.4	21.11	9	2	190	155	1.4	9.24	97.7	1
Buck	164.6	290.33	3	3	871	857	10.1	9.68	93.9	1
Cabin	132.7	35.50	4	2	142	150	3.9	8.51	96.7	1
Caledonia	142.5	29.60	10	6	296	252	5.5	8.42	96.9	1
Celestine	222.1	41.71	17	10	709	652	9.6	9.46	109.7	1
Christine	226.3	37.59	17	5	639	535	7.5	8.21	92.6	1
Cutt	126.6	16.10	21	10	338	297	6.9	8.76	86.3	1
Dorothy	265.2	55.25	8	1	442	442	7.9	8.65	98.6	1
Edith	303.1	30.25	4	1	121	87	1.2	7.67	103.1	1
Golden	80.9	13.70	20	15	274	264	6.3	8.52	92.6	1
Honeymoon	186.1	89.13	8	3	713	608	8.5	9.60	94.4	1
Horseshoe	306.7	32.75	8	2	262	261	0.7	7.97	107.4	1
Iris	248.5	42.10	10	1	421	456	8.1	7.88	100.2	1
J436	227.2	138.75	8	4	1110	1070	16.8	9.25	101.9	0
Leach	229.1	71.22	9	1	641	595	9.9	8.28	99.1	1
Little Honeymoon	50.4	87.25	4	2	349	365	4.4	7.67	66.9	0
Marjorie	289.0	25.56	25	4	639	606	10.4	8.38	98.8	1
16 ½ Mile	256.9	66.45	11	8	731	733	11.8	8.33	105.5	1
Mina	605.0	47.91	43	9	2060	1820	16.5	8.91	106.1	1
Moab	182.5	17.13	8	1	137	117	2.6	7.74	92.5	1
Osprey	108.1	44.00	2	1	88	101	0.4	9.23	97.1	1
Patricia	671.0	66.00	7	3	462	444	7.1	9.51	100.3	1
Pyramid	273.6	16.10	10	3	161	149	4.3	8.68	95.4	1
Virl	215.7	53.83	12	1	646	599	11.1	8.09	93.4	1

Abbreviations are total phosphorus (TP), total dissolved phosphorus (TDP), total nitrogen (TN), total dissolved nitrogen (TDN), dissolved organic carbon (DOC). In cases where concentrations were below detection limits, the detection limit was reported.

Table A-3.3 Environmental, physical and chemical variables from surveyed lakes and ponds in Waterton National Park (n=15)

Lake	Year	Julian Date	Elevation (m asl)	Annual mean air temperature (˚C)	Annual mean precipitation (mm)	Mean solar radiation (WH m^{-2})	Lake area (ha)	Catchment area (ha)	Catchment area/lake area
Alderson	2017	166	1811	-0.43	701.10	897442.93	11.75	107.75	9.17
Allison	2017	165	1274	4.00	537.35	856757.59	7.72	114.66	14.85
Bertha	2017	193	1774	0.73	684.25	898629.44	30.25	506.21	16.73
Buffalo Creek Pond	2017	165	1323	3.70	577.97	864692.70	0.85	737.97	867.79
Cameron	2017	164	1660	1.57	683.27	891296.69	141.01	792.01	5.62
Crandell	2017	196	1524	2.31	639.29	874508.43	6.09	121.10	19.89
Indian Springs W47	2017	165	1348	3.70	562.53	866987.37	2.30	56.23	24.48
Linnet	2017	195	1280	-0.20	601.42	854222.84	4.06	112.66	27.75
Lonesome	2017	195	1280	3.60	623.27	860382.36	15.69	394.65	25.15
Lost	2017	194	1875	0.40	695.77	883399.51	1.45	41.72	28.82
Lower Rowe	2017	192	1957	0.10	694.94	882170.97	1.76	35.53	20.15
Maskinongne	2017	196	1276	4.00	549.15	857504.56	53.74	1698.80	31.61
Summit	2017	164	1931	0.70	685.41	922941.53	1.88	42.37	22.56
Temporary Pond W60	2017	195	1293	3.80	560.00	865357.25	0.07	2.19	30.52
Upper Rowe	2017	192	2168	-0.60	711.60	905267.98	6.93	61.07	8.82

Table A-3.3 (continued)

Lake	**Vegetataion cover (%)**	**Barren land (%)**	**Catchment slope (˚)**	**Mixed sedimentary rock (%)**	**Non-carbonate sedimentary rock (%)**	**Carbonate sedimentary rock (%)**	**Maximum depth (m)**	**Secchi depth (m)**	**Surface water temperature (˚C)**
Alderson	20.76	34.73	36.71	100.00	0.00	0.00	60.0	7.0	3.0
Allison	86.73	8.44	2.72	0.00	100.00	0.00	2.4	0.9	15.3
Bertha	54.93	35.15	27.80	100.00	0.00	0.00	50.8	9.5	15.7
Buffalo Creek Pond	92.99	4.15	9.81	18.32	81.68	0.00	2.2	2.2	14.6
Cameron	59.86	13.41	22.56	69.03	5.95	1.00	39.0	5.0	4.6
Crandell	84.66	8.90	23.63	100.00	0.00	0.00	15.5	4.5	13.4
Indian Springs W47	91.06	4.70	4.62	0.00	100.00	0.00	4.0	3.5	15.2
Linnet	67.37	27.99	27.48	100.00	0.00	0.00	4.7	2.5	15.9
Lonesome	86.42	10.84	24.10	100.00	0.00	0.00	2.6	1.0	13.9
Lost	86.68	4.06	30.88	100.00	0.00	0.00	12.0	6.0	14.4
Lower Rowe	55.84	14.72	30.99	100.00	0.00	0.00	8.0	5.5	14.0
Maskinongne	94.40	3.86	3.31	0.00	100.00	0.00	2.0	1.0	13.7
Summit	94.64	0.00	7.85	100.00	0.00	0.00	2.3	2.3	1.9
Temporary Pond W60	82.35	17.65	2.90	100.00	0.00	0.00	1.6	0.5	19.6
Upper Rowe	52.59	25.86	24.36	100.00	0.00	0.00	3.0	3.0	15.4

Table A-3.3 (continued)

Lake	Conductivity (µS^{-cm})	TN:TP (mass)	TP (µg L^{-1})	TDP (µg L^{-1})	TN (µg L^{-1})	TDN (µg L^{-1})	DOC (mg L^{-1})	pH	Surface dissolved oxygen (%)	Fish (presence /absence)
Alderson	273.6	100.50	2	1	201	203	0.3	8.21	78.8	1
Allison	215.7	30.21	14	6	423	439	6.7	8.35	85.3	0
Bertha	379.6	4.92	12	43	59	103	5.0	9.80	107.4	1
Buffalo Creek Pond	120.6	26.00	10	1	260	235	3.4	8.97	97.6	1
Cameron	497.0	14.00	5	2	70	96	0.9	7.62	80.3	1
Crandell	581.0	20.88	8	1	167	152	2.5	8.355	86.8	1
Indian Springs W47	309.7	34.57	7	1	242	247	2.8	9.10	90.6	0
Linnet	135.5	17.18	11	1	189	139	2.1	8.61	91.5	1
Lonesome	345.7	37.30	10	7	373	393	7.9	8.71	89.9	0
Lost	287.4	9.57	7	6	67	71	1.2	9.33	88.5	0
Lower Rowe	107.4	16.00	5	2	80	42	0.7	9.98	88.5	0
Maskinongne	89.6	30.92	12	2	371	372	6.6	8.45	86.3	1
Summit	239.2	10.71	7	6	75	86	2.0	6.40	72.8	0
Temporary Pond W60	369.5	14.07	46	28	647	602	8.5	7.74	59.9	0
Upper Rowe	228.5	22.33	6	4	134	105	0.7	9.35	82.7	0

Abbreviations are total phosphorus (TP), total dissolved phosphorus (TDP), total nitrogen (TN), total dissolved nitrogen (TDN), dissolved organic carbon (DOC). In cases where concentrations were below detection limits, the detection limit was reported.

Table A-3.4 Environmental, physical and chemical variables from surveyed lakes and ponds in Yoho National Park (n=10)

Lake	Year	Julian Date	Elevation (m asl)	Annual mean air temperature (˚C)	Annual mean precipitation (mm)	Mean solar radiation (WH m^{-2})	Lake area (ha)	Catchment area (ha)	Catchment area/lake area
Celeste	2017	200	1997	-1.15	696.50	890780.31	2.13	18.74	8.82
Duchesnay	2017	199	1595	-0.52	681.95	843527.13	6.02	76.72	12.74
Hamilton	2017	199	2160	-2.62	723.98	911965.96	4.45	181.54	40.78
Hungabee	2018	205	2243	-3.00	698.81	926001.99	24.41	3301.72	135.27
Mary	2018	205	2034	-2.07	693.03	901502.02	53.61	952.96	17.78
Oesa	2018	205	2285	-3.48	699.52	928742.10	167.12	4783.21	28.62
Opabin	2018	205	2280	-3.00	698.96	930225.62	22.65	2618.64	115.62
Schaffer	2017	201	2170	-2.20	697.71	916953.30	1.26	107.31	85.36
Sherbrooke	2017	187	1803	-1.41	692.10	878046.16	36.14	2098.75	58.08
Wapta	2017	187	1595	0.26	685.86	854638.56	25.26	9577.80	379.10

Table A-3.4 (continued)

Lake	Vegetataion cover (%)	Barren land (%)	Catchment slope (˚)	Mixed sedimentary rock (%)	Non-carbonate sedimentary rock (%)	Carbonate sedimentary rock (%)	Maximum depth (m)	Secchi depth (m)	Surface water temperature (˚C)
Celeste	81.62	17.09	13.53	0.00	100.00	0.00	5.3	5.3	13.3
Duchesnay	85.40	10.08	21.53	0.00	100.00	0.00	1.3	1.3	16.4
Hamilton	3.25	93.77	30.91	0.00	64.67	35.33	12.0	5.0	7.2
Hungabee	24.65	65.91	34.36	0.44	89.67	9.90	2.7	2.2	14.4
Mary	31.95	60.93	30.99	0.00	100.00	0.00	3.5	4.0	14.5
Oesa	11.88	59.59	39.47	3.73	69.67	26.60	35.4	7.0	7.5
Opabin	13.47	73.52	36.41	0.55	86.97	12.48	12.3	6.0	10.1
Schaffer	46.60	48.98	25.22	0.00	72.69	27.31	2.5	1.9	6.7
Sherbrooke	39.34	49.69	26.73	0.74	50.46	48.81	12.0	2.5	9.2
Wapta	54.84	38.20	27.04	4.97	66.82	28.20	8.0	4.0	9.5

Table A-3.4 (continued)

Lake	Conductivity (μS^{-cm})	TN:TP (mass)	TP ($\mu g\ L^{-1}$)	TDP ($\mu g\ L^{-1}$)	TN ($\mu g\ L^{-1}$)	TDN ($\mu g\ L^{-1}$)	DOC ($mg\ L^{-1}$)	pH	Surface dissolved oxygen (%)	Fish (presence/ absence)
Celeste	164.1	7.22	9	1	65	89	0.6	7.77	100.00	1
Duchesnay	163.8	38.5.0	4	2	154	166	2.3	8.41	100.00	1
Hamilton	139.4	4.31	29	6	125	101	1.0	7.61	41.67	0
Hungabee	21.4	23.67	3	1	71	53	0.9	9.00	81.48	0
Mary	204.3	43.67	3	1	131	93	0.9	9.50	114.29	0
Oesa	149.2	15.50	8	7	124	114	0.6	9.04	19.77	0
Opabin	80.9	68.33	3	2	205	73	0.2	9.15	48.78	0
Schaffer	113.8	30.50	2	1	61	69	0.2	7.48	76.00	1
Sherbrooke	174.6	24.00	3	1	72	88	0.8	8.31	20.83	1
Wapta	170.6	46.50	2	3	93	95	0.3	8.26	50.00	1

Abbreviations are total phosphorus (TP), total dissolved phosphorus (TDP), total nitrogen (TN), total dissolved nitrogen (TDN), dissolved organic carbon (DOC). In cases where concentrations were below detection limits, the detection limit was reported.

Table A-3.5 Environmental, physical and chemical variables from surveyed lakes and ponds in Kootenay National Park (n=5)

Lake	Year	Julian Date	Elevation (m asl)	Annual mean air temperature (˚C)	Annual mean precipitation (mm)	Mean solar radiation (WH m^{-2})	Lake area (ha)	Catchment area (ha)	Catchment area/lake area
Cobb	2017	201	1260	0.93	667.13	826626.98	2.32	407.61	176.04
Floe	2017	199	2036	-2.01	693.10	902121.67	50.44	524.05	10.39
K20	2017	200	1218	1.60	583.66	820365.11	0.52	37.72	73.17
Kootenay Pond	2017	171	1188	1.50	585.17	821782.37	2.48	488.65	197.37
Olive	2017	199	1631	0.10	644.92	853647.08	1.75	44.04	25.23

Table A-3.5 (continued)

Lake	Vegetataion cover (%)	Barren land (%)	Catchment slope (˚)	Mixed sedimentary rock (%)	Non-carbonate sedimentary rock (%)	Carbonate sedimentary rock (%)	Maximum depth (m)	Secchi depth (m)	Surface water temperature (˚C)
Cobb	74.50	24.63	32.38	21.32	7.19	71.49	8.0	8.0	17.00
Floe	29.10	53.69	29.43	0.00	0.00	100.00	61.0	4.0	6.20
K20	99.34	0.00	4.88	0.00	100.00	0.00	3.5	2.5	18.00
Kootenay Pond	96.84	1.74	9.32	0.00	100.00	0.00	7.8	6.8	16.80
Olive	91.75	4.00	26.11	8.55	0.00	91.45	3.4	3.4	14.80

Table A-3.5 (continued)

Lake	**Conductivity (µS^{-cm})**	**TN:TP (mass)**	**TP (µg L^{-1})**	**TDP (µg L^{-1})**	**TN (µg L^{-1})**	**TDN (µg L^{-1})**	**DOC (mg L^{-1})**	**pH**	**Surface dissolved oxygen (%)**	**Fish (presence /absence)**
Cobb	379.6	6.48	61	58	395	401	5.3	8.11	90.8	1
Floe	120.6	14.56	18	14	262	284	3.5	8.99	81.7	1
K20	497.0	49.82	11	1	548	507	7.3	8.72	90.4	0
Kootenay Pond	581.0	50.20	5	2	251	241	2.2	8.16	109.5	1
Olive	309.7	72.50	2	1	145	322	1.5	8.18	96.0	1

Abbreviations are total phosphorus (TP), total dissolved phosphorus (TDP), total nitrogen (TN), total dissolved nitrogen (TDN), dissolved organic carbon (DOC). In cases where concentrations were below detection limits, the detection limit was reported.

Table A-3.6 Algal pigment concentrations derived from high-performance liquid chromatography (HPLC) for all sites within the Canadian Rockies (n=82). All data are presented in µg L^{-1}.

	Fucoxanthin	**Neoxanthin**	**Violaxanthin**	**Diadinoxanthin**	**Myxoxanthophyll**	**Alloxanthin**	**Diatoxanthin**	**Zeaxanthin**	**Lutein**	**Canthaxanthin**	**Chlorophyll *b***	**Chlorophyll *a***
Agnes	0.811	0.000	0.037	0.030	0.000	0.054	0.046	0.029	0.011	0.034	0.021	2.398
Baker	0.490	0.000	0.006	0.000	0.000	0.023	0.000	0.046	0.029	0.011	0.037	1.127
Boom	0.131	0.000	0.010	0.028	0.000	0.000	0.028	0.020	0.000	0.000	0.000	0.420
Copper	0.281	0.000	0.019	0.064	0.000	0.058	0.064	0.085	0.000	0.022	0.042	1.061
Eiffel	0.122	0.000	0.018	0.000	0.000	0.011	0.000	0.041	0.008	0.000	0.000	0.442
Grizzly	0.030	0.007	0.000	0.000	0.000	0.022	0.000	0.000	0.053	0.000	0.043	0.473
Herbert	0.097	0.000	0.016	0.026	0.000	0.047	0.026	0.046	0.013	0.000	0.000	0.546
Island	0.194	0.000	0.039	0.068	0.000	0.034	0.068	0.084	0.017	0.045	0.027	1.220
Kingfisher	0.380	0.000	0.014	0.090	0.000	0.121	0.090	0.172	0.038	0.000	0.000	1.308
Laryx	0.357	0.000	0.016	0.051	0.000	0.103	0.034	0.039	0.013	0.000	0.000	1.344
Lost (B)	0.043	0.000	0.000	0.000	0.000	0.028	0.000	0.014	0.016	0.000	0.000	0.335
Louise	0.062	0.000	0.000	0.000	0.000	0.000	0.000	0.025	0.000	0.000	0.000	0.227
Moraine	0.102	0.000	0.008	0.000	0.000	0.000	0.000	0.050	0.000	0.000	0.000	0.357
Mud	0.169	0.000	0.010	0.043	0.000	0.018	0.043	0.015	0.009	0.000	0.000	0.509
Mummy	0.055	0.000	0.006	0.015	0.000	0.042	0.021	0.034	0.012	0.000	0.022	0.472
O'Brien	0.890	0.000	0.046	0.193	0.000	0.147	0.193	0.073	0.124	0.000	0.100	3.735
Pilot	0.239	0.000	0.011	0.039	0.000	0.030	0.039	0.095	0.040	0.000	0.172	1.466
Pharaoh	0.906	0.000	0.037	0.034	0.000	0.064	0.024	0.099	0.026	0.000	0.127	1.964
Ptarmigan	0.208	0.000	0.013	0.027	0.000	0.045	0.027	0.067	0.027	0.006	0.085	0.990
Redoubt	0.075	0.000	0.006	0.026	0.000	0.014	0.026	0.011	0.020	0.000	0.000	0.313
Rockbound	0.180	0.000	0.013	0.016	0.000	0.012	0.044	0.094	0.004	0.000	0.022	0.650
Rock Isle	0.039	0.000	0.005	0.000	0.000	0.051	0.016	0.000	0.041	0.015	0.029	0.557
Sentinel	0.103	0.000	0.014	0.000	0.000	0.017	0.011	0.035	0.000	0.000	0.020	0.404
Smith	0.698	0.000	0.020	0.102	0.000	0.088	0.102	0.000	0.053	0.000	0.000	1.611
Taylor	0.392	0.022	0.035	0.068	0.000	0.055	0.068	0.000	0.192	0.000	0.366	2.231

Temple	0.357	0.000	0.016	0.320	0.000	0.013	0.320	0.027	0.000	0.000	0.032	1.873
Waterfowl	0.040	0.000	0.000	0.000	0.000	0.000	0.000	0.012	0.000	0.000	0.000	0.095
Annette	0.688	0.000	0.013	0.086	0.000	0.014	0.086	0.030	0.018	0.000	0.034	1.297
Beauvert	0.596	0.000	0.017	0.108	0.000	0.090	0.108	0.033	0.038	0.000	0.000	1.365
Buck	0.063	0.000	0.007	0.010	0.000	0.010	0.010	0.044	0.000	0.000	0.049	0.437
Cabin	0.098	0.000	0.012	0.020	0.000	0.012	0.020	0.040	0.000	0.000	0.016	0.484
Caledonia	0.100	0.000	0.025	0.033	0.000	0.153	0.033	0.104	0.020	0.000	0.076	1.525
Celestine	0.127	0.000	0.015	0.029	0.000	0.034	0.029	0.387	0.019	0.000	0.040	1.173
Christine	0.080	0.000	0.017	0.029	0.000	0.199	0.029	0.858	0.068	0.000	0.000	5.204
Cutt	0.217	0.000	0.018	0.040	0.000	0.051	0.040	0.227	0.000	0.010	0.022	1.097
Dorothy	0.198	0.000	0.015	0.058	0.000	0.038	0.058	0.127	0.012	0.000	0.000	0.878
Edith	0.273	0.000	0.011	0.085	0.000	0.033	0.085	0.021	0.026	0.000	0.013	0.611
Golden	0.291	0.000	0.018	0.046	0.000	0.035	0.046	0.094	0.000	0.000	0.030	0.974
Honeymoon	0.041	0.000	0.000	0.024	0.000	0.089	0.024	0.334	0.029	0.000	0.000	0.862
Horseshoe	0.423	0.000	0.014	0.097	0.000	0.052	0.097	0.100	0.000	0.030	0.195	1.605
Iris	0.202	0.000	0.009	0.066	0.000	0.081	0.066	0.286	0.041	0.015	0.000	1.878
J436	0.222	0.000	0.000	0.035	0.338	0.039	0.035	0.112	0.000	0.015	0.000	0.808
Leach	0.168	0.000	0.010	0.045	0.000	0.063	0.045	0.171	0.021	0.000	0.030	1.111
Little Honeymoon	0.076	0.000	0.013	0.035	0.000	0.008	0.035	0.033	0.012	0.000	0.000	0.461
Marjorie	0.367	0.000	0.016	0.066	0.000	0.054	0.066	0.120	0.034	0.000	0.039	1.715
Mile 16 1/2	0.175	0.000	0.007	0.068	0.000	0.025	0.068	0.030	0.011	0.000	0.000	0.805
Mina	0.000	0.000	0.046	0.000	0.000	0.462	0.000	0.830	0.395	0.000	0.000	0.000
Moab	0.264	0.000	0.012	0.101	0.000	0.028	0.101	0.050	0.010	0.007	0.102	1.463
Osprey	0.032	0.000	0.000	0.005	0.000	0.005	0.005	0.005	0.004	0.000	0.000	0.141
Patricia	0.083	0.000	0.005	0.033	0.000	0.057	0.033	0.056	0.013	0.000	0.000	0.474
Pyramid	0.163	0.000	0.011	0.025	0.000	0.044	0.025	0.047	0.015	0.000	0.016	0.786
Virl	0.703	0.000	0.034	0.141	0.000	0.060	0.141	0.209	0.027	0.000	0.118	2.289
Alderson	0.170	0.000	0.011	0.053	0.000	0.014	0.053	0.029	0.019	0.000	0.026	0.554
Allison	0.097	0.000	0.013	0.023	0.000	0.044	0.023	0.052	0.014	0.000	0.048	0.798

Bertha	0.757	0.000	0.015	0.087	0.000	0.148	0.087	0.041	0.056	0.000	0.033	1.934
Buffalo Creek Pond	0.049	0.000	0.014	0.000	0.124	0.029	0.000	0.079	0.000	0.000	0.030	0.381
Cameron	0.694	0.000	0.024	0.214	0.000	0.123	0.214	0.049	0.022	0.000	0.048	2.971
Crandell	0.394	0.000	0.015	0.114	0.155	0.058	0.114	0.060	0.014	0.000	0.056	1.281
Indian Springs W47	0.056	0.000	0.009	0.000	0.000	0.011	0.000	0.000	0.042	0.000	0.022	0.338
Linnet	0.576	0.000	0.073	0.169	0.000	0.000	0.169	0.000	0.255	0.000	0.130	2.265
Lonesome	0.044	0.000	0.011	0.000	0.092	0.000	0.000	0.000	0.047	0.000	0.047	0.447
Lost (W)	0.046	0.000	0.000	0.000	0.000	0.011	0.000	0.034	0.000	0.000	0.000	0.224
Lower Rowe	0.340	0.000	0.028	0.060	0.000	0.233	0.060	0.070	0.024	0.000	0.034	1.799
Maskinongne	0.139	0.000	0.021	0.026	0.000	0.013	0.026	0.023	0.000	0.035	0.000	1.488
Summit	0.027	0.000	0.011	0.000	0.000	0.000	0.000	0.000	0.022	0.000	0.023	0.137
Temporary Pond W60	0.213	0.019	0.084	0.000	0.000	0.311	0.000	0.000	0.314	0.000	0.268	3.636
Upper Rowe	0.205	0.000	0.034	0.046	0.098	0.066	0.046	0.093	0.010	0.019	0.000	0.751
Celeste	0.226	0.000	0.010	0.062	0.000	0.000	0.062	0.020	0.000	0.000	0.000	0.593
Duchesnay	0.069	0.000	0.008	0.000	0.000	0.000	0.000	0.030	0.000	0.013	0.026	0.728
Hamilton	0.571	0.000	0.010	0.083	0.000	0.034	0.083	0.000	0.026	0.000	0.000	1.376
Hungabee	0.109	0.000	0.021	0.065	0.000	0.008	0.022	0.084	0.000	0.000	0.064	0.607
Mary	0.122	0.000	0.026	0.011	0.000	0.013	0.004	0.018	0.007	0.000	0.017	0.465
Oesa	0.089	0.000	0.008	0.015	0.000	0.012	0.020	0.039	0.000	0.000	0.000	0.319
Opabin	0.589	0.000	0.014	0.089	0.000	0.058	0.220	0.025	0.014	0.000	0.020	1.608
Schaffer	0.034	0.000	0.000	0.006	0.000	0.000	0.006	0.008	0.000	0.000	0.000	0.097
Sherbrooke	0.142	0.000	0.012	0.000	0.000	0.000	0.000	0.024	0.000	0.000	0.000	0.496
Wapta	0.024	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.057
Cobb	1.713	0.000	0.038	0.245	0.124	0.115	0.245	0.061	0.000	0.000	0.000	3.641
Floe	0.040	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.098
K20	0.358	0.000	0.031	0.108	0.000	0.043	0.108	0.055	0.009	0.000	0.031	1.447

Kootenay Pond	0.037	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.031	0.000	0.000	0.296
Olive	0.062	0.000	0.000	0.023	0.000	0.000	0.023	0.000	0.000	0.000	0.000	0.173