Epilithic Algal Community Responses to Rapid Glacier Loss in the Canadian Rocky Mountains

by

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Abstract

Global melting of mountain glaciers is altering downstream ecosystems. As glaciers disappear, downstream water temperatures are rising while turbidity and nutrient concentrations decline. Here, knowledge gaps exist concerning how these abiotic changes will affect primary producers in glacial meltwater streams. I quantified abiotic variables and rock-attached algal communities termed epilithon in 10 stream sites along an environmental gradient of glacial influence in the Canadian Rockies. I hypothesized that physical factors would be the strongest predictors of community composition due to the damage incurred by biofilms from frequent scouring and abrasion events. Turbidity best explained an observed unimodal response of epilithic algal biomass accrual to glacial influence. However, abiotic variables poorly explained variation in community composition.

To further explore the impacts of glacial meltwater turbidity on epilithon, I designed a mesocosm experiment to test the effects of glacial flour, the primary determinant of turbidity in glacial streams, on algal community structure. Artificial stream channels were inoculated with algae and meltwater collected from a low turbidity glacial stream. Epilithic algal communities were then exposed to one of five turbidity levels by mixing varying amounts of glacial flour into meltwater. Moderate levels of turbidity significantly stimulated epilithic algal biomass accrual relative to the effects of low and extreme turbidity treatment levels, appearing to favor growth by chlorophytes over that of diatoms and other chromophytes. Potential explanations of low biomass accrual by epilithon to low and extreme turbidity involved nutrient limitation and physical disturbance, respectively.

My findings suggest that the turbidity of glacial streams has a strong influence on the growth and diversity of algal biofilms. I expect that further glacier loss will suppress epilithic algal growth in glacial meltwater streams due to declining nutrient availability and heightened exposure to damaging levels of ultraviolet radiation. Since algal growth supports the productivity of glacial meltwater ecosystems in the absence of terrestrial subsidies from surrounding barren alpine landscapes, I anticipate that loss of glaciers could in certain cases impair the downstream productive capacity for harvestable coldwater fishes.

Preface

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Chapter 1: Glacial stream ecosystems and epilithic algal communities under a warming climate

Abstract

Climate change is accelerating the global loss of glaciers with potentially striking consequences for downstream ecosystems. However, there exists limited evidence of the ecological impacts of glacier loss in meltwater streams, particularly in those outside of North America and Europe. We provide a review of the abiotic conditions in glacial streams that are potential factors of their ecosystem function and biodiversity with an emphasis on their key primary producers, namely rock-attached algae or "epilithon". Here, shrinking glaciers discharge over time less turbid melt waters, resulting in slower moving and more transparent stream conditions that are also warmer and more chemically dilute. We hypothesize that these environmental changes will stimulate epilithic algal growth while also shifting its community structure towards larger and less nutritious taxa. Although such an increase in algal growth may benefit the productive harvestable fish capacity of certain mountain streams, a potential negative trade-off involves the proliferation of nuisance algae (e.g., Didymosphenia geminata), which thrives under clear, nutrient-poor mountain conditions. We advocate the use of long-term ecological monitoring programs and experiments coordinated across global mountain ranges to better predict and understand the ecological consequences of loss of glaciers on mountain stream ecosystems.

Key words: alpine streams, benthic algae, climate change, glacial loss

Introduction

What does the future hold for glacial stream ecosystems as their sources diminish across mountains around the world? This question is of urgent importance given the accelerating rates of climatic warming and glacier loss around the world (Zemp et al. 2019; Hugonnet et al. 2021). Widespread negative glacier mass balances have been recorded across mountain regions over the past several decades (Zemp et al. 2019; Hugonnet et al. 2021). Glacier recession has further accelerated in the 21st century, compounding losses globally (Hugonnet et al. 2021). In North America, these trends suggest that many mountain glaciers could disappear by 2100 (Clarke et al. 2015; Zemp et al. 2019). Evolving alongside glaciers, glacial stream ecosystems have also entered a period of rapid environmental change (Brown et al. 2007; Slemmons et al. 2013; Fell et al. 2017; Hotaling et al. 2017; Milner et al. 2017; Brighenti et al. 2019; Cauvy-Fraunié and Dangles 2019; Elser et al. 2020). Warmer, slower, and less turbid conditions are expected in glacial headwater streams as hydrological inputs from snowmelt, groundwater, and rain replace declining contributions of turbid meltwater from shrinking glaciers. However, relatively little is known of the ecological impacts of glacial recession on downstream ecosystems. To date, limnological reviews of these glacial influences have focused mainly on planktonic communities in lakes (e.g., Saros et al. 2010; Sommaruga 2015; Elser et al. 2020)to microbes and invertebrates in streams ecosystems (e.g., Rott et al. 2006; Hotaling et al. 2017; Brighenti et al. 2019; Elser et al. 2020). However, knowledge gaps exist concerning the cumulative impacts of rapidly melting glaciers on primary producers that are essential to the unique biodiversity and functioning of glacial headwater ecosystems. There is also a need to integrate evidence from various mountain regions around the world into our understanding of stream ecosystem responses to glacier loss given differences in their geological histories, anthropogenic stressors, and rates of glacial ablation. For example, glacial coverage is more extensive across western North America than in the European Alps (Fig. 1), it is also experiencing much greater glacier loss rates than in Europe (Zemp et al. 2019). This discrepancy highlights the need to further study glacial stream biota in regions such as western North America given the known effects of glacier loss on aquatic biodiversity (Cauvy-Fraunié and Dangles 2019). The scope of our review focuses on the physical and chemical environments that exist in glacially fed streams and then examines the limited evidence of the effects of abiotic variables on the algal component of rock-attached biofilms termed epilithon. Here, epilithic algae are the key primary producers supporting secondary production in streams situated above treelines (i.e., alpine; Rott et al. 2006). We posit that glacial ablation will result in the amelioration of headwater stream conditions (e.g., less hydrological variation and warmer, less turbid surface waters) so as to promote greater epilithic algal diversity and function.

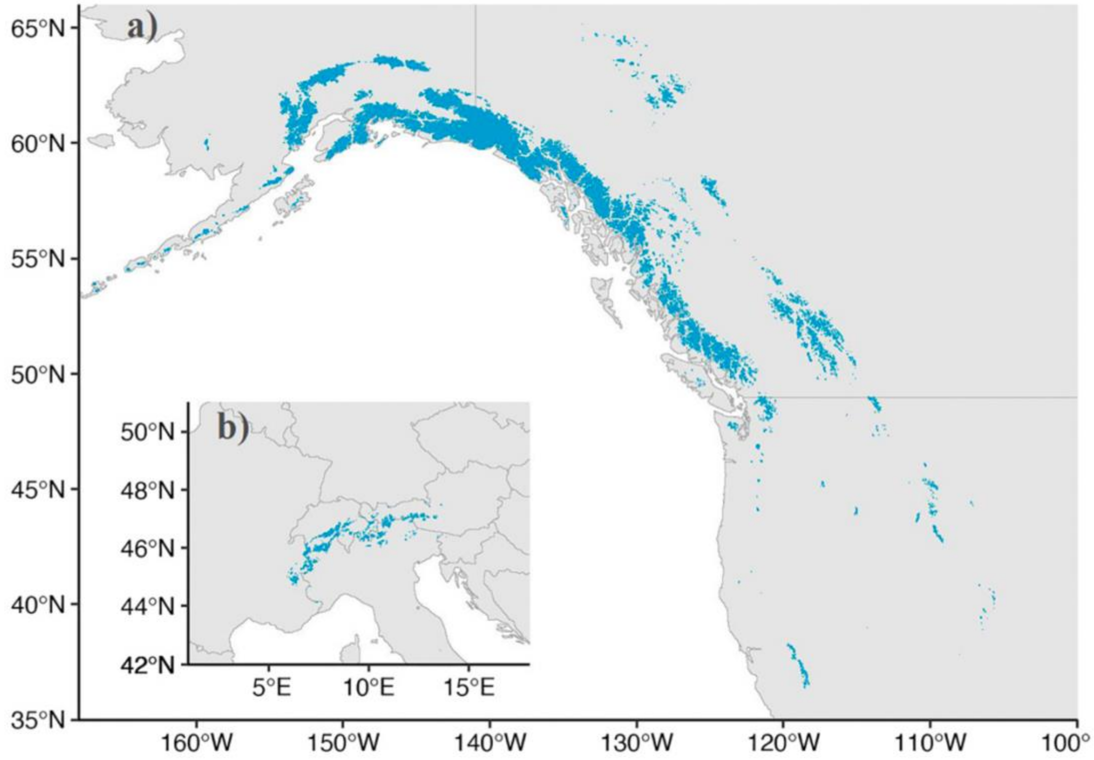

Figure 1.1. Glacial coverage across (a) western North America below the Arctic circle and (b) central Europe. Data was taken from the Global Land Ice Measurement from Space database (GLIMS and NSIDC 2005). Base map data was taken from South (2022). Coordinate reference system used is WGS 84.

The abiotic environment of glacial streams

Glacial meltwaters form extreme lotic alpine environments that are distinct other alpine streams fed more by groundwater and snowmelt sources (Brown et al. 2003). High discharges throughout summer, near-freezing temperatures, highly turbid waters, and low organic nutrient concentrations are amongst the conditions inherent to meltwaters. Glacier loss will subsequently alter meltwater environments, as conditions increasingly resemble those of nonglacial streams.

Meltwater dynamics

Glacial meltwater streams show extreme diurnal variation in discharge rates as they cascade through alpine environments. Daily flow patterns are most pronounced during the summer months (Smith et al. 2001; Lafrenière and Sharp 2003; Hannah et al. 2007; Kneib et al. 2020). Warm summer afternoons accelerate glacial melt rates, producing afternoon discharge pulses. These daily flow patterns are complicated by stochastic rain events as heavy rainfall can dramatically raise stream flow in a matter of hours causing unexpected increases to stream flow (Lafrenière and Sharp 2003; Kneib et al. 2020). Glacial streams also exhibit seasonal variation in discharge rates. Meltwater discharge rates vary with seasonal air temperature patterns which shape distinct flow periods (Moore et al. 2009; Miner et al. 2017). In winter, consolidation of snow and ice replenishes glacial mass lost to melt. Here, cold temperatures limit the production of glacial meltwater, limiting stream flow for several months (Smith et al. 2001). During this time, glacial streams rely on glacial base flows or non-glacial groundwater. Intermittent flows are also possible if glacial base flows, or alternative water sources, are absent from catchments (Robinson et al. 2016). As spring arrives, mountain snowpack melt supplies water to glacial streams. Snowmelt inputs accelerate flows, producing similar discharge rates to those during peak glacial melt periods. By late summer, glaciers have replaced snowmelt as the primary source of water to glacial streams. This shift corresponds to a peak in stream discharge as large amounts of water previously trapped as ice are released downstream. Flows slow again in the fall as air temperatures drop and glaciers cease to melt. These seasonal flow patterns result in a distinct annual hydrograph for glacial streams, highlighted by peak flows in summer. At the scale of decades to millennia, variation in glacial meltwater supply underlies the predicted transition from fast-flowing lotic conditions to slower stream flows (Huss and Hock 2018). To begin, increased glacier melt will augment the supply of meltwater to glacial streams, sustaining rapid summer flows. Meltwater production is expected to reach a maximum rate at intermediate stages of glacier loss, an apex known as “peak water” (Huss and Hock 2018). After peak water is reached, meltwater production will decline, resulting in slower, shallower streams (Milner et al. 2017; Huss and Hock 2018). This diminished water supply from glaciers is expected to push seasonal discharge peaks earlier into melt seasons (Brahney et al. 2017). Similarly, stochastic flow patterns are hypothesized to replace seasonally deterministic discharge peaks as precipitation events become more influential to stream flow (Milner et al. 2017). For glacial streams lacking snow or groundwater inputs, the frequency of intermittent flows could increase because of inconsistent meltwater supply (Paillex et al. 2020). Glacier loss could even reroute streams within glacial catchments, diverting flow from historical channels into novel paths across deglaciated landscapes (Shugar et al. 2017).

Natural melt cycles drive turbulent glacial streambed environments. Unstable channels are common in summer as high discharges transport cobble downstream (Boix Candell et al. 2021) and create turbulent streambed boundary layers (Cauvy-Fraunié et al. 2014). The magnitude and frequency of these disturbances are heightened in glacial streams compared to other alpine stream types because of the large volume of water released by glaciers over short seasonal periods (Milner et al. 2001; Boix Candell et al. 2021). Rapid summer discharges also suspend fine glacially eroded rock material within the water column (Moore et al. 2009). When carried downstream, this particulate matter, also known as rock or glacial flour, shear the streambed below by grinding against larger anchored stones.

As glaciers receded, decreased meltwater production will promote stable stream channels less prone to disturbance (Hannah et al. 2007; Fell et al. 2018). Slower and lower flows associated with groundwater and snowmelt inputs will incite fewer streambed movement events (Boix Canadell et al. 2021). Here, reduced surges in meltwater will lessen physical disturbance or "tumbling" of submerged rocky substrates (e.g., cobbles), thereby enabling them to become better consolidated into the streambed. The movement of glacial flour and other suspended sediments within streams will also decline, creating less turbid streams subject to fewer scouring events (Kneib et al. 2020; Boix Canadell et al. 2021). The predicted decline of meltwater supply will subsequently alter the thermal, light, and nutrient properties of glacial streams, transforming their abiotic environment.

Thermal dynamics

Glacial ablation is predicted to result in warmer downstream reaches (Milner et al. 2017; Brahney et al. 2021). Glacial streams are typically frigid environments (Brown et al. 2005). Long, snow- and ice-covered winters, and short summers replete with meltwater inputs limit glacial streams to often near-freezing temperatures. The cold states of alpine freshwaters are the product of interactions between air temperature, snow- and glacier-melt, groundwater, rain, and internal heat capacity (Smith et al. 2001; Brown et al. 2005; Hannah et al. 2007; Brown and Hannah 2008; Milner et al. 2017; Kneib et al. 2020). Near glaciers, water temperatures rarely exceed 2 ◦C year-round, even in the summer months, as consistent meltwater inputs negate warmer air temperatures (Brown et al. 2003; Brown et al. 2005). Temperature profiles warm downstream from glaciers as meltwater mixes with warmer groundwater and snowmelt inputs (Smith et al. 2001). The thermal mosaic created by these water sources produces stark downstream temperature patterns along glacial streams. For example, Brown et al. (2005) recorded a mean temperature increase of 7 ◦C along a one kilometer transect of a glacial stream in the French Alps. Glacial streams also display thermal depth gradients, where streambed temperatures are cooler than stream surfaces (Brown et al. 2005).

Rising stream temperatures are expected as meltwater supply lessens with glacier loss. Certain glacial streams have already warmed significantly in Western Canada since 1983 (Brahney et al. 2021), as well as in Alaska and the Swiss Alps (Milner et al. 2008; Finn et al. 2010). Diminished inputs of meltwater promote higher temperatures as thermal dynamics become increasingly determined by warmer snow and groundwater sources (Brahney et al. 2021; Brown et al. 2003; Brown and Hannah 2008; Fellman et al. 2014). For example, Brahney et al. (2021) found that low-influence glacial streams had mean August temperatures of above 10 ◦C, compared to high-influence streams that consistently remained below 10 ◦C. While low temperatures will likely persist near glacial margins (Brown and Hannah 2008), historical temperature trends (Fell et al. 2018), and meltwater input comparisons (Brahney et al. 2021) both suggest a warmer future for glacial streams.

Spectral irradiance

Glacial loss will expose streams to increased solar irradiance as extended windows of water clarity allow light to further penetrate glacial streams (Elser et al. 2020). Clear streams are expected to succeed highly turbid flows that prevent light from reaching streambeds because of their high loads of glacial flour and other suspended sediments (Boix Canadell et al. 2021)(Fig. 2.). Although most incoming light is readily scattered by these particles (Martyniuk et al. 2014;

Rose et al. 2014), light that successfully reach streambeds can be divided into two components: ultraviolet radiation (UVR) and photosynthetically active radiation (PAR). These entities are differentiated by their wavelength with UVR being shorter (~290–400 nm) than PAR (~400–700 nm) (Rose et al. 2014). Considering PAR and UVR availability depends on the level of turbidity, the spectral landscape of glacial streambeds often co-varies with seasonal glacial stream turbidity patterns.

Figure 1.2. Contrasting glacial streams in the Canadian Rockies. Glacial ablation will result in a state change from high turbidity (left) to increasingly clear stream conditions (right). Photo credit: Karson Sudlow.

Winters flows are relatively clear, allowing light to consistently reach streambeds (Smith et al. 2001; Boix Canadell et al. 2021). Although, if streams are covered by winter snowpack's, snow can replace turbidity as a significant barrier to light availability (Uehlinger et al. 2010; Boix Canadell et al. 2021). Snow and glacier melt in spring and summer, respectively, highlight an extended period of turbid, lowlight conditions within glacial streams (Uehlinger et al. 2010; Martyniuk et al. 2014; Boix Canadell et al. 2021). These turbid conditions persist until fall when turbidity declines, enabling higher light intensities to reach streambeds. Mountain landscape features, like canyons, steep mountain faces, and aspect, can accent the seasonal light regimes of glacial streams by shadowing streams (Boix Canadell et al. 2021). Likewise, the vegetative development of streamside banks can intercept incoming light during summer months (Vannote et al., 1980). These factors limit the supply of light to glacial streams. Glacier loss will promote less turbid stream conditions, exposing streambeds to greater intensities of UVR and PAR (Boix Canadell et al. 2021). Less turbid conditions, historically limited to fall, and winter if streams remain open, will extend into summer and spring as the supply of turbid meltwater declines and slower flows encourage stable streambeds (Uehlinger et al. 2010). Input of less turbid meltwaters should result in the underwater light environment in glacial streams more resembling that found in snow- and groundwater-fed streams (Boix-Canadell et al. 2021). Subsequently, development of soils and vegetation in previously glaciated areas under a warming climate will input dissolved organic matter into these streams, thereby potentially helping attenuate potentially harmful UVR (Williamson et al. 2001; Elser et al. 2020). More research is here needed to quantify how the spectral qualities of alpine headwaters change and affect their ecology during glacial ablation (Elser et al. 2020).

Meltwater chemistry

Glacial ablation will alter the supply of inorganic and organic nutrients to meltwater stream ecosystems. Nitrogen is mostly present in glacial streams as inorganic nitrate, nitrite, and ammonia. Two main sources support the supply of nitrogen into glacial streams: atmospheric deposition and microbial nitrification (Slemmons et al. 2013). Nitrogen is readily deposited onto alpine glaciers and snowpack's through atmospheric cycling. These deposits then enter meltwater during seasonal melt periods. Atmospherically derived nitrogen may be particularly prevalent in mountain regions with heavy anthropogenic land use (Fegel et al. 2016). Microbial communities living below glaciers also provide nitrogen to glacial streams (Baron et al. 2009). Autochthonous nitrogen production via microbial nitrification produces inorganic nitrogen pools within subglacial sediments. These pools are frequently flushed by meltwater moving through subglacial channels into glacial streams. Similar nitrification by microbial communities on and adjacent to glaciers further compliment the biotic nitrogen supply to glacial streams. These processes support the typically elevated nitrogen concentrations of glacial streams compared to their non-glacial alpine freshwaters (Lafrenière and Sharp 2005; Saros et al. 2010; Slemmons et al. 2013; Warner et al. 2017; Colombo et al. 2019).

Glaciers also support phosphorus cycling in meltwater streams. Movement of glaciers atop of geological formations can erode rock containing phosphorus (Hodson et al. 2008). Glacially derived phosphorus is bound to glacial sediment and is transported into glacial streams via meltwater, leading to large fluxes of inorganic phosphorus during melt seasons (Hodson et al. 2008; Uehlinger et al. 2010; Brahney et al. 2021). Weathering of glacial bedrock and recently exposed glacial sediments may also contribute phosphorus to streams within glaciated catchments (Hood and Scott 2008; Hood and Berner 2009; Vinšová et al. 2022).

Adsorbed to glacial flour and other sediments, most phosphorus is considered to not be bioavailable in glacial streams (Hodson et al. 2008). Nevertheless, concentrations of soluble reactive phosphorus are relatively higher in glacial streams than in those fed by snowmelt or groundwater (Hood and Scott 2008; Hood and Berner 2009; Boix Canadell et al. 2021; Brahney et al. 2021; Marytniuk et al. 2022). Like inorganic phosphorus, soluble reactive phosphorus is likely supplied through erosion and other subglacial weathering processes. As such, glaciers appear to positively influence soluble reactive phosphorus availability, as heavily glaciated catchments often contain higher concentrations than streams receiving little meltwater. For example, soluble reactive phosphorus concentrations were highest in heavily glaciated catchments along a glacial influence gradient of Alaskan glacial streams (Hood and Berner 2009). However, many other studies were unable to detect a relationship between glacier influence and bioavailable phosphorus (Rinke et al. 2001; Uehlinger et al. 2010; Warner et al. 2017; Fell et al. 2018). These inconsistent patterns necessitate further research to quantify biologically relevant phosphorus supply to meltwater as glaciers disappear.

Dissolved organic matter as operationally defined as dissolved organic carbon (DOC) in glacial streams is mainly autochthonous. Microbial communities living on, below, and within glaciers and meltwater streams are the sources of this relatively translucent DOC (Lafrenière and Sharp 2003; Hood et al. 2009). Microbially derived DOC is also relatively labile because of its high protein to lignin ratios relative to those of DOC derived from allochthonous (i.e., terrestrial) sources (Hood et al. 2009). While microbial communities produce labile autochthonous DOC, total DOC supply is often limited within glaciated catchments as they lack allochthonous subsidies from nearby barren alpine environments (Lafrenière and Sharp 2003; Hood et al. 2009; Li et al. 2018; Brahney et al. 2021).

The nutrients supplied to meltwater streams by glacial processes are predicted become increasingly scarce as glaciers disappear. Both soluble reactive phosphorus and nitrogen derived from glacial or subglacial deposits could decline as ice retreats (Warner et al. 2017; Brahney et al. 2021). While regional differences in bedrock weathering and atmospheric nutrient cycling could compensate these losses (Baron et al. 2009), many glacial streams could become increasingly nutrient poor. Warner et al. (2017) found that nitrate concentrations were an order of magnitude larger in glacial streams than nearby snow-fed streams in the American Rocky Mountains. Soluble reactive phosphorus is also predicted to become increasingly scarce as glaciers disappear. Negative soluble reactive phosphorus trends have been noted in North American (Brahney et al. 2021; Hood and Scott 2008)and European (Fell et al. 2018) glaciated catchments. In contrast to waning nitrogen and phosphorus supply, meltwater DOC concentrations should increase as catchments become increasingly vegetated, supporting allochthonous carbon pools (Hood and Scott 2008). Frigid meltwater discharge and its chemistry along with high turbidity characterize the distinct abiotic environment of glacial streams. These abiotic conditions then constitute the factors that are expected to determine the structure of epilithic communities in glacial streams.

Epilithic algal communities of glacial streams

Glacial stream ecosystems rely on highly specialized communities of algae for primary production within otherwise energy-barren glacier forefields covered by ice, snow, and rock. Epilithic biofilms composed of diatoms, cyanobacteria, chrysophytes, and chlorophytes, grow on the substrate of glacial streambeds globally. In these relatively sparse alpine landscapes, epilithon is a primary food source for consumers given the absence of abundant allochthonous resources (Zah et al. 2001; Rott et al. 2006; Niedrist and Füreder 2018). In addition to their role as a key trophic resource, epilithon facilitate other ecological processes in glacial streams, such as decomposition (Kohler et al. 2022) and nutrient cycling (Busi et al. 2022). These processes maintain ecosystem functioning critical to the flow of energy through glacial streams. Yet, emerging novel meltwater, thermal, spectral, and nutrient regimes alter algal communities and their functioning in glacial streams, with further changes hypothesized as glaciers continue to disappear (Rott et al. 2006; Uehlinger et al. 2010; Brahney et al. 2021).

Meltwater dynamics

Epilithon strongly reflect the highly variable and fast water velocities that are common to glacial streams (Uehlinger et al. 1998; Rinke et al. 2001; Cauvy-Fraunié et al. 2016; Fell et al. 2018). Constrained by these scouring events, epilithon in glacial streams are often limited to disturbance tolerant species. Biggs et al. proposed that algal communities in disturbance-prone streams compose a functional group characterized by early colonizers with fast growth rates, low biomass, and small cell sizes (Biggs et al. 1998). These traits confer both resistance and resilience, as small cells with low biomass are better equipped to tolerate abrasion and quick growth rates facilitate recolonization after particularly damaging disturbances. Although algal responses and adaptations to flow in alpine streams are rarely explicitly tested, Biggs et al.'s

(1998) disturbance paradigm is critical to understanding algal community structure within rapid glacial streams.

Fast water velocities expose epilithon to strong drag forces (Biggs et al. 1998; Rott et al. 2006). Species with outward growth forms that protrude into the water column, such as filamentous cyanobacteria, incur increased drag because of their large surface area and are easily detached from streambeds by rapid flows (Biggs et al. 1998; Rott et al. 2006). To mitigate these drag forces many species found in fast flowing streams, like those fed by glacial meltwater, rely on simple colonial or unicellular life forms with small surface areas. These growth forms convey tolerance to flow speeds damaging to most other species (Biggs et al. 1998; Rott et al. 2006; Lange et al. 2016). Likewise, strong attachment abilities and prostrate growth forms further limit damage from rapid flows (Hieber et al. 2001; Lange et al. 2016). Species with strong attachment abilities, such as the diatoms A. minutissimum and Hannaea arcus, and the chrysophyte Hydrurus foetidus, are commonly found in fast-moving mountain streams (Fell et al. 2018; Hieber et al. 2001; Rott et al. 2006). These adaptive traits enable epilithic algae to tolerate the rapid summer flows of glacial streams.

Extreme flow conditions are a key filter of algal diversity within glacial streams (Rott et al. 2006; Gesierich and Rott 2012; Fell et al. 2018). Epilithon found in headwaters near glacial margins are highly tolerant to swift meltwaters. These communities are composed of few species with strong attachment abilities and compact life forms (Hieber et al. 2001; Gesierich and Rott 2012; Fell et al. 2018). For example, channel stability covaried with diatom diversity in a space-fortime study of European glacial streams (Fell et al. 2018). In their study, Fell et al. (2018)

found that unstable streams heavily influenced by glaciers supported a limited number of pioneer species with simple growth forms. In comparison, weakly attached species with morphologically diverse growth forms dominated communities within stable, low glacial influence streams. Interestingly, community composition is relatively stable across seasonal flow patterns (Hieber et al. 2001; Uehlinger et al. 2010). A possible explanation for this lack of temporal species turnover could be that while channel disturbances initially sort species assemblages, species capable of passing through the disturbance filters of glacial streams are relatively unaffected by subsequent changes to stream flow. However, more studies are needed to test the impacts of streamflow on algal community assembly.

Like diversity, algal growth is also affected by the rapid flows of glacial streams. Biomass accrual is severely limited in glacial streams during months of high flow as frequent disturbances constrain biofilm development (Uehlinger et al. 1998; Hieber et al. 2001; Uehlinger et al. 2010; Boix Canadell et al. 2021). During these disturbance-prone periods, algae may limit their growth, persisting in diminished states to avoid detachment (Rott et al. 2006). The arrival of fall coincides with rapid biomass accumulation as fast growth rates allow epilithon to quickly capitalize on favorable flow conditions (Hieber et al. 2001; Rott et al. 2006). While several studies explain biomass accrual with slowing discharges (Hieber et al. 2001; Uehlinger et al. 2010; Khamis et al. 2016; Boix Canadell et al. 2021), Cauvy-Fraunié et al. (2016) cemented the importance of flow by experimentally testing the effects of glacial meltwater suppression on epilithon. Cauvy-Fraunié et al. (2016) found that glacial flow suppression significantly increased algal biomass. Reduced flow likely relieved algae from the frequent scouring and instability caused by rapid glacial meltwater.

More productive and diverse epilithic communities are expected to as glaciers melt. The establishment of stable streambeds promote the colonization of species previously filtered from turbulent glacial streams (Biggs et al. 1998; Fell et al. 2018). As water velocity slows, loosely attached and tall algae (e.g., filamentous forms) are better able to colonize stable streambed substrate (Fell et al. 2018). Otherwise, these growth forms are sensitive to high shear stress and are often restricted to streams with low flow (Lange et al. 2016). Therefore, glacier loss should increase epilithic diversity through the recruitment of stalked diatoms (e.g., Gomphonema spp.) and filamentous cyanobacteria (e.g., Phormidium spp.) and chlorophytes more commonly found in higher-order mountain streams receiving snow- and groundwater inputs (Hieber et al. 2001; Rott et al. 2006; Gesierich and Rott 2012; Fell et al. 2018). Slower water velocities are also expected to stimulate epilithic biomass. As the severity and frequency of streambed movement events and scouring decline, more stable, low flow conditions are conducive to biomass accumulation, enabling the accumulation epilithic biomass (Uehlinger et al. 2010; Boix-Canadell et al. 2021). For example, alpine groundwater streams with lower flows contain greater epilithic biomass than glacial streams, likely due to fewer spates (Boix-Canadell et al. 2021). Epilithic biomass should increasingly resemble biomass patterns common to other alpine stream types as glacial discharge declines.

Thermal dynamics

Epilithic algae are well adapted to survive the cold waters of glacial streams and temperature is likely not a key factor determining community composition (Rinke et al. 2001; Rott et al. 2006; Uehlinger et al. 2010; Robinson et al. 2014). Ubiquitous cellular adaptations and plastic metabolic requirements allow many species to survive cold environments, including glacial streams (Morgan-Kiss et al. 2006; Busi et al. 2022). Algal biomass accrual has been observed in glacial streams across seasons, including winter when stream temperatures are consistently near 0 ◦C(Uehlinger et al. 2010). Likely, epilithic growth can occur in glacial streams when water temperatures are above 0 ◦C(Rott et al. 2006).

Although the relative importance of grazing macroinvertebrates to epilithon in glacial streams is not well documented, rising water temperatures may indirectly affect the algae by increasing grazing pressure. Here, macroinvertebrates rely on autochthonous food sources epilithon for food as allochthonous subsidies from glaciated alpine environments are rare (Zah et al. 2001; Niedrist and Füreder 2016). Thus, increased grazing pressure may partially offset release from physical scouring that epilithon experience with declining meltwater velocity. In situ experiments are needed to test if higher water temperatures will cause shift from abiotic to biotic control of epilithon during decline of glacial meltwater inputs into alpine streams.

Little is known whether warmer meltwaters due to glacier loss will stimulate epilithon. Recent evidence from the European Alps indicates that long-term meltwater warming trends are associated with increased diatom biodiversity (Fell et al. 2018). However, in North America where streams are also warming, epilithon-temperature relationships remain untested. Explicit experiments are further needed to determine if stream warming alters algal growth and diversity in glacial meltwaters.

Solar irradiance

To survive within glacial streams, epilithon must tolerate frequent and extreme fluxes in solar irradiance. The variable turbidity of glacial streams affects the underwater penetration of PAR, which then affects epilithic primary production (Uehlinger et al. 2010; Boix-Canadell et al. 2021). However, despite often low PAR intensities, epilithic growth can occur in turbid streams (Martyniuk et al. 2014) as it does elsewhere in clear streams (Uehlinger et al. 2010; Boix-Canadell et al. 2021). Chromatic acclimation involving increased production of light-harvesting pigments likely maintain algal growth in turbid environments while at the same time glacial flour helps attenuate and possibly scatter harmful UVR (Martyniuk et al. 2014.). In fact, epilithic algal biomass can be higher in more turbid glacial streams likely because of the alleviation of UVR-photoinhibition by rock flour (Martyniuk et al. 2014).

Uehlinger et al. (2010) identified spring and fall as seasons where increased light availability could stimulate epilithic growth. However, few intra-annual monitoring studies are carried out, rendering it difficult to confirm if these photoperiods promote algal growth. It is especially difficult to isolate the effect of light on algal productivity as periods of stream clarity often also coincide with increased streambed stability. Boix Canadell et al. (2021) found that above a threshold of streambed movement, seasonal light regimes were inconsequential with regards to glacial stream primary productivity. A similar pattern was found in Canadian glacier-fed montane streams (Bowman et al. 2007). Whether light is a key influence on epilithic biomass, or secondary to channel stability in glacial streams, remains unknown.

Light availability should also alter the nutritional quality of epilithon within glacial streams. According to the light:nutrient hypothesis, increased light exposure should decrease the nutritional quality of algae as carbon fixation outpaces the assimilation of limiting nutrients (Sterner et al. 1997). However, the high light intensities epilithon experience in clear glacial streams produce the opposite response. In Patagonian glacial streams, epilithon from clear meltwaters have lower carbon:nutrient ratios than communities from turbid habitats (Martyniuk et al. 2019). Shading experiments over transparent streams also increased epilithic carbon:nutrient ratios as biofilms were released from photoinhibitive light intensities (Martyniuk et al. 2019). Here, high UVR and PAR exposure likely limits algal growth while increasing cellular nutrition content. As higher trophic levels likely rely on epilithic food sources, these results suggest that increased light exposure could benefit trophic energy transfer within glacial streams as they progressively clear with glacier loss.

Few studies have explored how solar irradiance affects the taxonomic and trait-based composition of epilithic communities in glacial streams. Certain species have specialized photosystems adapted to low light availability in mountain streams (Aigner et al. 2018). For example, the colonial cyanobacteria Chamaesiphon polonius commonly found in glacial streams has low light requirements compared to other Chamaesiphon species found in clear water habitats (Aigner et al. 2018). High turbidity conditions likely exclude epilithic algae requiring high light intensities by reflecting and attenuating incoming solar radiation. Complementary to species-specific light requirements, functional trait approaches involve algae possessing erect and tall morphologies to be at a competitive advantage for harvesting light as they can extend up through biofilms to occupy the upper canopy of epilithon (Biggs et al. 1998). For example, filamentous and chain-forming benthic algae can shade out lower canopies of adnate and prostrate taxa. However, complex growth forms are rarely found in glacial streams due to rapid meltwater flows (Rott et al. 2006; Gesierich and Rott 2012). Therefore, morphological trait differences between communities in glacial streams should emerge because of differences in streambed stability rather than light availability.

Glacier loss will increasingly expose stream epilithon to the potentially harmful intensities of PAR and UV that are present at alpine environments (Elser et al. 2020). However, if increased light exposure will harm or benefit epilithon is unknown. Martyniuk et al. (2014) observed that reduced turbidity in South American glacial streams slowed periphytic algal growth, likely due to photoinhibition. Low biomass was also reported in Tibetan glacial streams, likely due to highly turbid waters (Murakami et al. 2012). Elsewhere, experimental evidence showed that UVR suppressed epilithic biomass accrual by impairing growth by the diatom Achnanthidium minutissimum in a clear alpine lake (Vinebrooke and Leavitt 1996). However, increased light exposure can also increase epilithic productivity and biomass (Boix Canadell et al. 2021; Uehlinger et al. 2010). For example, Boix Canadell et al. (2021) observed that alpine streams fed by snow and groundwater inputs received greater amounts of PAR along streambeds than glacial streams. Increased PAR stimulated primary productivity and biomass in these non -glacial streams. Historical light conditions are likely important in determining algal responses to clearing glacial streams, as photo-adaptations to light availability should influence responses increased light availability. More research is needed to determine how changing light conditions impact epilithon in glacial streams.

Meltwater chemistry

Nitrogen and phosphorus supplied by glacial processes support the nutrient requirements of epilithon in glacial streams. Although nutrient concentrations are often lower in glacial streams than in most aquatic environments, glaciermediated supply likely satisfies the requirements of relatively sparse epilithon. Low biomass, and thus limited nutrient uptake rates, could be insignificant enough to deplete even scarce nutrients. Several nutrient addition experiments have failed to stimulate algal growth within glacial streams (Rinke et al. 2001; Gafner and Robinson 2007). For example, neither artificial phosphorus nor nitrogen additions explained algal biomass differences in Swiss glacial streams (Rinke et al. 2001). Conversely, artificial nutrient additions altered epilithic biomass and composition into low-flow Antarctic glacial streams (Kohler et al. 2016). Thus, like light, nutrients are likely a secondary filter to epilithon compared to physical disturbances.

The supply of bioavailable nutrients, particularly bioavailable phosphorus, to glacial streams is expected to decline as glaciers disappear (Milner et al. 2017). However, the consequences of this predicted nutritional drought on epilithon are little studied. Many algal species are capable mediating low nutrient availability. For example, several cyanobacteria species rely on heterocysts to fix nitrogen during periods of nitrogen limitation (Kumar et al. 2010). Similarly, algae can increase their phosphatase activity, which cleaves phosphates from substrates and organic material, to alleviate phosphorus limitation (Dyhrman 2016). Several studies demonstrate induced phosphatase activity in epilithon under phosphorus limiting conditions, including in Patagonian and Canadian rivers receiving glacial meltwater (Bowman et al. 2005; Martyniuk et al. 2022). Whether these adaptations are sufficient to supplement the loss of glacier-supplied nutrients is not known. If not, then algal communities could be increasingly limited to species with plastic nutrient requirements and constrained growth forms.

Future challenges

Will warmer, less turbid meltwaters with slower and more stable water velocities benefit epilithic growth within glacial streams as glaciers disappear? As hypothesized by Uehlinger et al. (2010), accelerated glacier melt should result in a longer duration of environmental conditions that stimulate algal biomass accrual (Fig. 3). Growing seasons previously isolated to the autumn months could extend into summer as stream channels stabilize following earlier meltwater peaks. These sustained low flow states should stretch potential growth windows from weeks into months because of fewer and less severe disturbance events. Such shifts towards earlier and longer windows of opportunity have already been reported within North American glacial streams undergoing substantial glacier loss (Brahney et al. 2021), and are predicted to continue into the 21st century (Bellmore et al. 2022). New opportunities to accrue algal biomass in spring could further complement increased growth during the autumn if low flows follow accelerated winter snowpack melt. While algal growth during the spring months has been observed in European glacial streams (Rott et al. 2006; Boix Canadell et al. 2021), further studies are needed to determine whether glacier loss improves potential algal growth prior to the melt season. Ultimately, meltwater states increasingly like snow- and groundwater-fed alpine streams should stimulate epilithon as glaciers disappear.

While slower, warmer flows could promote algal growth and colonization in glacial streams, certain changes could stress epilithic communities. Elser et al. (2020) hypothesized that warmer temperatures will accelerate the enzymatic activity, and thus metabolism, of species within glacial streams. Simultaneously, the nutrients supplied by glaciers, like nitrogen and bioavailable phosphorus, needed to fuel cell function will become increasingly scarce. Limited downstream nutrient supply could underwhelm the energetic demands of epilithon. Increased recruitment of downstream species into glacial streams will further compound the nutrient requirements of epilithon, highlighting the likelihood of nutrient scarcity as glaciers recede. Decreased meltwater turbidity could also negatively affect epilithon. As glacial streams shift to less turbid states, intense solar irradiance penetrates further into glacial streams (Boix Canadell et al. 2021). Prolonged exposure to intense levels of UVR and PAR at alpine elevations could increase photoinhibition (Martyniuk et al. 2014; Aigner et al. 2018). Whether these stressors dampen, or even negate, the emergence and expansion of further growth opportunities for algae is not well understood.

Of similar concern is the potential loss of specialized epilithic diversity as glaciers disappear. Algal communities within glacial streams are composed of relatively few, highly specialized species. As glaciers melt, the establishment of moderate conditions like warmer temperatures and stable streambeds promote the colonization of species previously filtered from glacial streams, improve local stream diversity (Rott et al. 2006; Gesierich and Rott 2012). However, increased colonization will likely coincide with the disappearance of glacial specialists from regional species pools (Fell et al. 2018). Although colonizers lack the resistance traits needed to withstand the severe influence of meltwater, they possess superior competitive abilities compared to the specialized species common in glacial headwaters. Therefore, glacier loss could instigate the removal of unique algal species from glacial streams as cosmopolitan generalists common in snowand groundwater-fed streams outcompete specialist species for limiting resources. Indeed, although Fell et al. (2018) observed that streams with low glacial influence hosted more diverse communities of diatoms, specialist species were often absent despite dominating communities in harsher meltwater streams. Specialized diversity loss and species turnover in response to melting glaciers is not unique to epilithon. Regional macroinvertebrate species loss is well documented in glacial streams across the world (Jacobsen et al. 2012). Similar patterns have also been reported in microbial communities (Wilhelm et al. 2013). Although more studies are needed to corroborate specialized diversity loss in epilithic communities, the parallel decline among adjacent trophic levels is alarming.

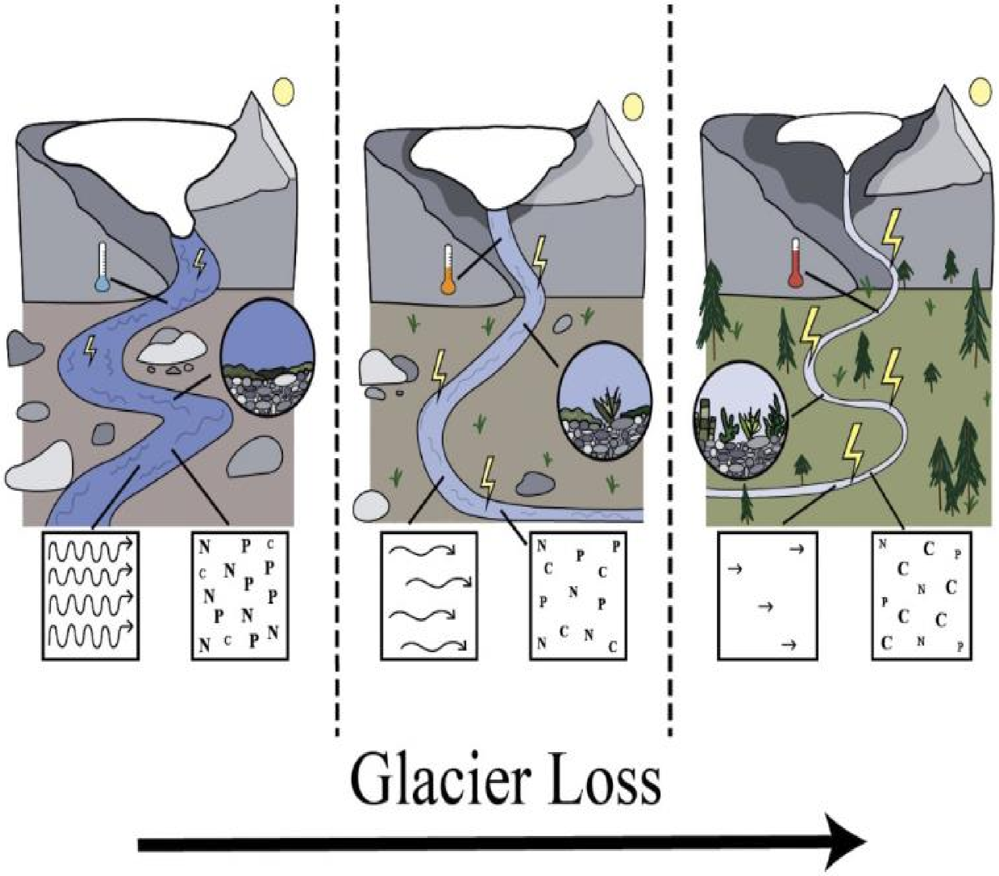

Figure 1.3. Conceptual progression from left to right of impacts of glacial recession on stream dynamics involving meltwater discharge (bottom left insert), water temperature (thermometer),

solar irradiance (lightning bolt), water chemistry (bottom right insert), and epilithic algal succession (Huss and Hock 2018). The illustrated progression shows stream ecosystems becoming less turbid (Boix Canadell et al. 2021), warmer (Brahney et al. 2021), and in depleted in nitrogen and phosphorus concentrations compared to carbon with the decline in turbid glacial meltwater discharge (Warner et al. 2017; Elser et al. 2020). Slowing water velocity promotes epilithic biodiversity by enabling erect filamentous green algae and cyanobacteria to colonize adnate and prostrate diatom-dominated communities (Rott et al. 2006). As turbid meltwater discharge rates decline, less hydrologic shearing force combined with less turbid and warmer water conditions that increase underwater light availability and length of growing season also stimulate epilithic production (Uehlinger et al. 2010; Boix Canadell et al. 2021; Brahney et al. 2021).

Glacier loss could also alter the ecological functions algae provide to glacial stream ecosystems. Epilithic cycling of nutrients and decomposition of organic matter fuel higher trophic levels in depauperate glacial streams. Because of the low algal diversity within glacial streams, these functions are maintained by relatively few highly specialized species. Hypothesized diversity loss could therefore disrupt the ecological functions maintained by specialized epilithic algae if replaced by downstream generalists. However, recent evidence suggests that ecological functions, some maintained by algae, are enhanced in streams with reduced glacier influence (Kohler et al. 2022). For example, benthic microbes were more enzymatically active in streams under weakened glacial influence globally (Kohler et al. 2022). Kohler et al. (2022) posited that as glaciers disappear, food webs within glacial streams transition from “grey” chemolithotrophic bacteria dominant food webs to “green” ones driven by photoautotrophs, like epilithon. As such, glacier loss could emphasize epilithon’s role as basal energy producers, particularly in streams lacking allochthonous resource subsidies.

Lastly, glacial streams increasingly resembling snowmeltand groundwater-fed streams could affect the nutritional quality of epilithic algae for consumers. Epilithic algae in turbid glacial streams are highly nutritious due in part to their organic content, which enables grazing macroinvertebrates to attain larger body masses than similar taxa can in warmer, less turbid streams (Niedrist et al. 2018). However, glacial turbidity can also lower the nutritional quality of epilithon by relieving photoinhibition, thereby promoting fixation of inorganic carbon relative to uptake of nutrients, such as nitrogen and phosphorus (Martyniuk et al. 2014). Subsequently, declining glacial meltwater inputs might result in stimulation of epilithic algal production to offset nutrient limitation in grazers by providing them with increased algal food availability (Boix-Canadell et at. 2021). These differing potential scenarios call for explicit experiments to conducted that explore the effects of rapidly melting glaciers on trophic transfer efficiencies of carbon and nutrients in alpine headwater streams.

Conclusion

This review adds to the body of knowledge dedicated to a unified conceptual framework to predict biological responses to rapidly changing glacial streams. Though reviews of macroinvertebrates in glacial streams already exist (Jacobsen et al. 2012; Milner et al. 2001), similar appraisal are needed for epilithon given their foundational role within alpine freshwater ecosystems. To conclude, we present the following suggestions as a template to guide future research of epilithon in glacial streams.

1. Increase experimental approaches when studying epilithic responses to glacier loss. Although alpine environments render it difficult to perform field experiments, more explicit hypothesis testing will advance our mechanistic consequence of glacier loss on epilithon. We point to creative experimental approaches by Cauvie-Fraunié et al. (2016)andDrost et al. (2022) to address the effects of predicted flow suppression on glacial stream benthos as inspiration for future experiments. Likewise, artificial shading experiments over Patagonian glacial streams

have significantly advanced our understanding of how algae respond to alpine light gradients (Martyniuk et al. 2014; Martyniuk et al. 2019). Experimental approaches simulating glacier loss scenarios will be increasingly important as glacial environments continue to deteriorate.

2. Determine if glacial streams support rare algal species. Little is known if epilithic biodiversity within glacial streams is unique, or if most species are ubiquitous across environments. Recent evidence suggests that glacial streams harbour specialized macroinvertebrate biodiversity unique to alpine waters (Muhlfeld et al. 2020). Whether certain algae are restricted to glacial streams has yet to be determined. Further exploration of algal biodiversity within meltwaters could identify potential species at risk and inform future conservation initiatives for alpine freshwaters.

3. Coordinated distributed experiments across global mountain regions, particularly in ranges outside of Europe, are needed to further develop mechanistic hypotheses about glacier loss impacts on epilithon. Fell et al. (2018) highlighted the need for studies from diverse glaciated regions to determine whether global conceptual models can be built for algal response to glacial loss, or if regional differences structure algal communities within glacial streams. Ranges needing further study include the Himalayas and Andes. Addressing this point will also contribute to the description of specialized algal biodiversity noted in point 2.

4. Concerns have emerged whether glacier loss will promote the presence of nuisance algal species within glacial streams. As glacial stream conditions ameliorate, the potential for colonization by competitively dominant species could increase, altering ecosystem function. For example, Brahney et al. (2021) found that decreased glacier influence promoted the proliferation

of the nuisance diatom Didymosphenia geminata in Canadian mountain streams. While D. geminata blooms do not appear to alter fish growth or feeding (Clancy et al. 2021), little is known about how it impacts their spawning habitat and reproductive success (Brahney et al. 2021). If blooms were associated with negative fitness consequences for fish, significant resources would be required to remove D. geminata from glacial stream ecosystems. We suggest increased monitoring of glacial streams in regions susceptible to nuisance species would help prevent the need for intensive management.

5. Lastly, the potential for glacier loss to create new habitat and resources for freshwater species, like Pacific salmon, as meltwater conditions improve is an exciting frontier in alpine ecology (Pitman et al. 2020; Pitman et al. 2021; Bellmore et al. 2022). Although abiotic shifts will no doubt ameliorate the potential for downstream invertebrates and fishes to colonize glacial streams, increased recruitment will require robust trophic foundations. If epilithon within glacial streams are productive and nutritious enough to support expanding grazer populations remains unknown. Building upon research by Uehlinger et al. (2010), intra- and interannual investigations into epilithic biomass responses to glacier loss could improve our understanding of how glacier loss alters the productive capacity of glacial streams to support higher trophic levels Glacial stream ecosystems have entered an era of significantly accelerated environmental change driven by rapid loss of glaciers. Previously defined by brief epilithic growing seasons, glacial streams are expected to transform into increasingly productive habitats if hydrologically compensated by inputs of groundwater and snowmelt. Simultaneously, disappearing glaciers may impoverish meltwater epilithic diversity by impairing endemic coldwater taxa and enabling colonization by more competitive algae from warmer environments. These poorly understood

opposing dynamics highlight the potential complexity of ecological responses by glacially formed alpine streams to a rapidly warming climate. Essential to the functioning of glacial streams, the fate of these primary producers underlies the stability of these unique alpine ecosystems. Understanding the impacts of glacier loss on epilithon is critical to the functioning and conservation of alpine ecosystems as glaciers continue to shrink and disappear during the 21st century.

Main Research Objectives:

1. Identify the environmental predictors of algal community composition responses to glacier loss in glacial streams (Chapter 2)
2. Experimentally test for the effects of glacial flour on epilithic algal communities from glacial streams (Chapter 3)

To achieve objective 1, I surveyed the epilithic algal communities and the physio-chemical conditions of 10 sites within five catchments experiencing glacier loss in the Canadian Rockies. I implemented a space-for-time study design to quantify the relative influence of glaciers as % glacier coverage upstream of each site. Algal community compositions were identified with high-performance liquid chromatography of diagnostic pigment abundances. Significant environmental predictors of algal community composition and biomass were identified using multivariate (RDA), linear, and non-linear models.

To achieve objective 2, I designed a stream mesocosm experiment at the University of Alberta. I tested the effects of five levels of meltwater turbidity on algal growth using artificial communities taken from a clear glacial streams. Each treatment was replicated four times and the experiment ran for five weeks. The effects of turbidity on pigment-inferred community abundances were analyzed using a repeated measures ANOVA.

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Chapter 2: Environmental predictors of epilithic algal communities in alpine streams along a deglacialization gradient

Introduction

Widespread glacier loss across mountain regions globally is altering downstream ecosystems (Huggonet et al., 2021; Milner et al., 2017; Zemp et al., 2019). Negative mass-balance rates have accelerated in the 21st century, pushing glaciers towards tipping points, known as "peak water", where the supply of meltwater begins to decline until their sources vanish entirely (Huss and Hock, 2018). Diminishing meltwater supply is expected to reconfigure glacial streams from abiotic states historically defined by near 0°C temperatures, turbulent discharges during summer melt seasons, high loads of suspended sediment, and low organic nutrient content towards environments that resemble snow- and groundwater-fed alpine streams (Brown et al., 2003; Elser et al., 2020; Milner et al., 2017; Sudlow et al., 2023; Uehlinger et al., 2010). Now, glacial streams are becoming increasingly warm and clear, with lower flows and higher organic matter (Elser et al., 2020; Milner et al., 2017; Sudlow et al., 2023). Consequentially, this transition has affected communities living with glacial streams as compositions of highly specialized species tolerant of the extreme meltwater environments are incrementally replaced by downstream generalists (Cauvy-Fraunié and Dangles, 2019; Fell et al., 2018; Jacobsen et al., 2012).

For epilithic algae attached to glacial streambeds, ameliorating meltwater conditions due to glacier loss have altered community diversity and growth. Algal community composition in glacial streams is primarily shaped by disturbance-related meltwater conditions such as turbidity and discharge (Fell et al., 2018; Rott et al., 2006). Specialized diatoms well suited to tolerate these harsh flows because of their small cell sizes and strong attachment abilities (Fell et al., 2018; Rott et al., 2006). However, increasingly moderate disturbance regimes due to glacier loss have promoted colonization of generalist diatoms as well as other algal groups, such as chrysophytes, cyanobacteria, and chlorophytes (Fell et al., 2018; Hieber et al., 2001). Glacier loss has also impacted the growth of epilithic algal communities (Boix Canadell et al., 2021; Uehlinger et al., 2010). Despite harsh meltwaters limiting biomass accrual throughout large portions of the year, "windows of opportunity" drive increased production in fall when glacial melt slows, disturbance intensity decreases, and increased light reaches streambeds. Glacial loss is hypothesized to extend this period into summer, potentially benefiting the productivity of these ecosystems (Bellmore et al., 2022; Uehlinger et al., 2010). Although primary producers in alpine streams have received increased research interest in recent years (Bellmore et al., 2022; Boix Canadell et al., 2021; Busi et al., 2022; Fell et al., 2018), community responses inclusive of non-diatom groups to glacier loss are not well understood. Likewise, evidence needed to identify the environmental predictors driving biodiversity and growth shifts as glacial streams transition abiotic states remains limited. Further research is now needed to holistically characterize how glacier loss impacts algal communities in glacial streams given their central role in ecosystem function.

Algae are a crucial component of meltwater ecosystems (Busi et al., 2022). Highly glaciated catchments often lack substantial terrestrial vegetation which limits allochthonous inputs of organic matter into streams channels. Instead, algae, along with other microorganisms, act as the dominant primary producers in glacial streams. Here, algae, along with bacteria and fungi, provide high-quality food sources that sustain higher trophic groups to otherwise nutritionally sparse waterscapes (Busi et al., 2022; Niedrist et al., 2018). Similarly, algae decompose organic material in glacial streams, further contributing to bioavailable carbon stocks downstream (Kohler et al., 2022). In addition to algae biodiversity and growth, recent evidence suggests that glacier loss also alters the functions primary producers provide to glacier stream ecosystems (Fell et al., 2021; Kohler et al., 2022; Niedrist et al., 2018). For example, Kohler et al. (2022) identified that retreating glaciers accelerated benthic biofilm decomposition in meltwaters as environmental harshness declined. Conversely, glacier loss can alter the food quality algae provide to macroinvertebrates as biofilms are increasingly composed by downstream generalists with low nutritional value (Niedrist et al., 2018). Although these findings have added to our understanding of how glacier loss impact lower trophic levels in glacial streams, research explicitly focused on epilithic algae will further clarify the contributions of primary producers to glacial stream ecosystems.

I used a space-for-time approach to study how glacier loss alters epilithic algal community composition and biomass in glacial streams across five catchments experiencing glaciation in the Canadian Rockies. I hypothesized that along a gradient of glacial influence, disturbance-related environmental predictors bests explain shifts to the composition of epilithic algae communities. As glacial influence decreases, less turbid, slow flowing streams should result in shifts from diatom-dominated biofilms to increasingly diverse communities composed of algal groups with low disturbance tolerances, such as chlorophytes and filamentous cyanobacteria (Hieber et al., 2001; Rott et al., 2006). Decreased disturbance should allow for generalist species with diverse life history traits to colonize new habitats as they become less environmentally extreme (Fell et al., 2018; Giesierich et al., 2012; Rott et al., 2006). I also expected that decreased glacial influence increase epilithic community biomass due to declining meltwater turbidity. Highly turbid streams scour epilithic biofilms while scattering photosynthetic active radiation (PAR), preventing the accumulation of biomass through photosynthesis (Boix Canadell et al., 2021; Rose et al., 2014; Uehlinger et al., 2010). This study aims to address existing knowledge gaps regarding biotic responses to glacier loss by characterizing the diversity and biomass of epilithic algal biofilms in a region where glaciers are predicted to largely disappear (Zemp et al., 2019).

Methods

Study Area

My study took place on the eastern slopes of the Rocky Mountains within Banff and Yoho National Parks, Canada. Glaciers cover an estimated 1351.7 Km^2 of this region (Bolch et al., 2010). Western Canada is experiencing some of the largest negative glacier mass-balances globally (Zemp et al., 2019), with up to 90% of glacier area predicted to disappear by the end of the century (Clarke et al., 2015). These features make the Canadian Rocky Mountains an ideal location to study how glacier loss alters alpine stream ecosystems.

Site Identification

Google Earth and Global Land Ice Measurements from Space database (GLIMS and NSIDC, 2005, updated 2018) were used to identify candidate streams. Specific sites were selected to control for the absence of upstream lakes that moderate potential glacial influence (Hieber et al., 2001). Where possible, I also tried to mitigate the presence of non-glacial tributaries which can further influence meltwater environments (Brown et al., 2003). With these parameters accounted for, I identified ten sample sites within five catchments along a 100 km latitudinal gradient

(Table 2.1; Figure 2.1). This gradient extended from Lake Louise, Alberta in the south northwards to Saskatchewan Glacier, Alberta. Watershed size and percentage of glacier coverage (i.e. % glacier influence) were then determined using a 25m resolution digital elevation model of the region the Watershed tool in ArcMap^{TM} 10.8.1 (Alberta Environment and Parks, 2017; Natural Resources Canada, 2015). Glacier influence for these sites ranged from 1.6% to 36.1% (Table 2.1).

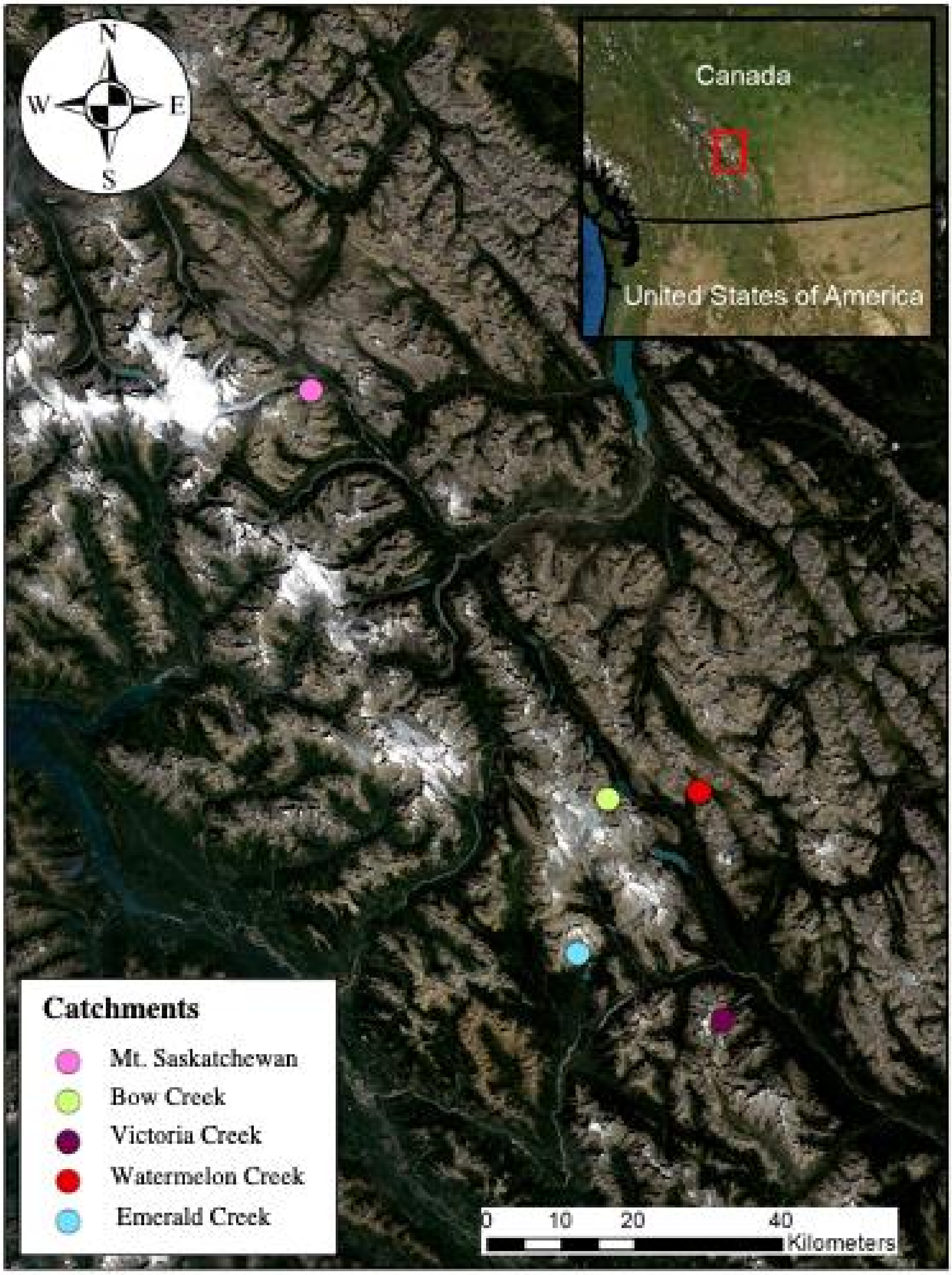


Figure 2.1. Map of catchment locations in the Canadian Rocky Mountains. Base map taken from ArcMap World Imagery. Source credits: Esri, Maxar, Earthstar Geographics, and the GIS User Community. Map projection is WGS 1984 UTM Zone 11N.

Table 2.1. Site name and locations

Site	Latitude	Longitude	Elevation	% Glacier Influence
Bow Down	51.659074	-116.48896	2010	8.2
Bow Up	51.63645	-116.48383	2209	26.5
Emerald Down	51.4702	-116.55046	1487	13.6
Emerald Left	51.47084	-116.55115	1498	1.9
Emerald Right	51.471	-116.55077	1497	28.2
Saskatchewan	52.15826	-117.07195	1904	19.8
Victoria Down	51.3947	-116.25828	1911	26.3
Victoria Up	51.38894	-116.26809	1925	36.1
Watermelon Down	51.66688	-116.31178	1984	1.6
Watermelon Up	51.66706	-116.30975	2053	2.3

Field Sampling

Catchments were sampled in August 2022. Glacier melt rates within the study region are typically highest in August, with meltwater contributing an increased proportion of river flow across the province of Alberta (Anderson and Radić, 2020). Each catchment was sampled at an upstream and downstream location, if possible, to capture the longitudinal differences in stream environments. However, Mt. Saskatchewan was only sampled in one location due to safety concerns. Each site was resampled every seven days for a total of four visits to account for differing stream conditions across the melt season. Mt. Saskatchewan was inaccessible on August 18th and was subsequently sampled twice more (August 25th and 30th) to ensure equal sample sizes across sites.

Water temperature (°C), dissolved oxygen (mg/L), turbidity (Nephron Turbidity Units), pH, and specific conductivity were measured with a YSI Exo2 Sonde. A 50 mL unfiltered water sample was collected at each site and stored at 4°C to measure total phosphorus (TP) and total nitrogen (TN). Another 50 mL of stream water was filtered through Whatman 0.45um cellulose acetate syringe filters and stored at 4°C to collect dissolved nutrient water samples. This included total dissolved nitrogen (TDN), total dissolved phosphorus (TDP) and dissolved organic carbon (DOC). An additional two 12 mL filtrate samples were frozen to measure soluble reactive phosphorus (SRP) and nitrate/nitrite concentrations (NO_2/NO_3). All water chemistry bottles were rinsed three times with their respective end member before filling for quality control.

Epilithic algal samples were collected from 20 hand-sized cobbles randomly selected along a cross-section of a wadable riffle zone at each site. A plastic 18.75 cm^2 template was placed on each cobble, within which algae were removed by scrubbing for 30 seconds with an Oral B 500 sonicated toothbrush. Once scrubbed, each cobble, the toothbrush head, and any algal residue were rinsed into an enamel pan with 50ml of deionized water to form an algal slurry. Ten of these slurries were then transferred to 60ml falcon tubes and preserved with 10 drops of Lugol's solution and stored at 4°C for later taxonomic identification. The remaining 10 slurries were filtered through 0.45um Whatman filters using a filter tower and hand pump to concentrate algal pigments. Filters were then placed into petri dishes and immediately placed on ice until stored in a -20 °C freezer. All equipment was thoroughly rinsed with stream water between samples.

Laboratory Analysis

Chemical analyses of all water samples were conducted at the Biogeochemical Analytical Services Laboratory at the University of Alberta. TN, TDN, SRP, TP, TDP, and NO2/NO3 were analyzed using a Lachat QuikChem 8500 FIA Automated Ion Analyzer. DOC was analyzed using a Shimadzu 5000A TOC analyzer.

Five randomly selected frozen algal pigment samples from each sampling date were prepared and analyzed by High Performance Liquid Chromatography (HPLC) following the protocol reported by Cook et al. (2023). Average pigment concentrations, reported as ug / cm^2, were calculated between replicates for each pigment for each sampling data. Chlorophyll *a* (chl *a*) was used as an approximate estimate of total epilithic algal biomass (Baulch et al., 2009). Taxonomically diagnostic pigments, mainly fucoxanthin, diatoxanthin, diadinoxanthin, violaxanthin, zeaxanthin, neoxanthin, and chlorophyll *b*, were used to estimate the relative abundance of major algal groups according to Wright et al. (2005) (Table 2.2).

Table 2.2. Diagnostic pigments and their corresponding algal groups. Chromophytes are representative of chrysophytes and diatoms.

Pigment	Algal group
Chlorophyll *a*	Total biomass
Chlorophyll *b*	Chlorophytes
Diatoxanthin	Diatoms
Diadinoxanthin	Chromophytes
Fucoxanthin	Chromophytes
Zeaxanthin	Cyanobacteria
Canthaxanthin	Cyanobacteria
Myxoxanthin	Colonial cyanobacteria
Violaxanthin	Chlorophytes

An additional five randomly selected algal taxonomic samples from each sampling occasion were selected and pooled together to create to composite sample that was sufficiently representative of the epilithic community. Samples were vigorously shaken for 30 seconds to suspend cells before pipetting 1mL from each into a representative sample for each site. This representative sample was homogenized again before pipetting 0.108 mL into Palmer counting slide. All cells in the counting chamber were enumerated under 400x magnification using a light microscope. Algae were identified down to genus level using Wehr et al. (2015). However, due to low cell counts and poor taxonomic resolution, taxonomic analysis was considered low quality and not included in this analysis.

Statistical analysis

Prior to analysis, environmental (water temperature, dissolved oxygen, turbidity, pH, and specific conductivity) and water chemical data (TP, TDP, TN, TDN, NO_2/NO_3, and SRP) was assessed for normality following the procedures outlined in Zuur et al (2010). Turbidity, TP, TN, and TDN were subsequently log-transformed to account for skewness. Statistical correlations were assessed using a Pearson correlation matrix and % dissolved oxygen was subsequently dropped from the analysis due to strong collinearity water temperature ($r^2 = 91$). Chl *a* was also log-transformed to down-weight the influence of outliers observed sporadically across the melt season. Diagnostic pigment concentrations were transformed using a Hellinger transformation to account for a large proportion of zeros across our dataset and to down-weight rare pigment concentrations (Legendre and Gallagher et al., 2001). For water chemistry samples where concentrations fell below detectable levels, half of the detection value was used for analyses (Antweiler and Taylor, 2008). DOC was dropped from analysis due to a high proportion of below detection values.

I inferred causal effects of glacial influence on physio-chemical stream environment using linear regression. Principal Component Analysis (PCA) was then used to visualize and assess shared variation between variables along principal component axes. Environmental variables were then constrained against diagnostic pigment concentrations using redundancy analysis (RDA) to identify significant environmental predictors of the relative abundance of major algal groups. Correspondence Analysis (CA) of diagnostic pigment concentrations identified that a linear ordination approach was suitable as the length of axis 1 was less than 3 standard deviations (axis 1 length = 0.71 S.D.). Prior to ordinating diagnostic pigments, week 1 and 3 site visits to Victoria Down were removed from analyses due to insufficient data. All parameters were also scaled and centered. The statistical significance of the ordination was assessed using an analysis of variance permutation test (alpha = 0.05). If the ordination proved statistically significant, forward selection based on adjusted R^2 with 9999 permutations was then used to identify significant explanatory environmental variables. The effects of environmental conditions and water chemistry on algal biomass (i.e., chl *a* concentration) were explored using linear regression and generalized additive models. Model fit was assessed using AIC. Here, if the AIC difference between non-linear and linear models for a given relationship was less than 2, the more parsimonious linear model was selected. All statistical analyses were performed using the *vegan* package in R Studio version 2021.09.1 (Oksanen et al., 2020).

Results

3.1 - The meltwater environment

Table 2.3: Mean environmental (a) and chemical (b) conditions at each study site across four visits in August 2022. Water chemistry parameters reported as µg/L.

a)

Site	**Glacier Influence (%)**	**Water Temperature (°C)**	**pH**	**Specific Conductivity (µs/cm)**	**Turbidity (NTU)**	**Velocity (m/s)**
Watermelon Down	1.63	8.46	7.76	186.45	2.14	0.80
Emerald Left	1.86	9.21	7.65	128.50	49.81	0.64
Watermelon Up	2.35	7.05	7.59	171.88	1.01	0.95

Bow Down	8.16	8.70	7.75	123.35	20.73	0.98
Emerald Down	13.63	9.02	7.74	122.35	18.33	0.98
Saskatchewan	19.79	5.41	7.66	154.88	63.65	0.90
Victoria Down	26.25	2.01	8.04	109.37	491.59	0.97
Bow Up	26.45	5.68	7.59	101.35	16.23	0.75
Emerald Right	28.17	7.45	7.57	119.43	6.86	0.94
Victoria Up	36.07	1.16	8.01	110.57	546.95	1.22

b)

Site	**Glacier Influence (%)**	**TP**	**TDP**	**SRP**	**NO_2/NO_3**	**TN**	**TDN**
Watermelon Down	1.63	3.00	2.50	2.00	134.00	62.25	58.25
Emerald Left	1.86	10.75	1.13	1.25	82.25	34.50	51.00
Watermelon Up	2.35	4.67	3.00	2.25	102.75	74.67	70.50
Bow Down	8.16	8.50	1.67	1.00	53.67	40.00	49.67
Emerald Down	13.63	5.00	1.50	0.75	71.50	39.00	45.75
Saskatchewan	19.79	26.50	2.00	1.50	122.00	31.25	70.50
Victoria Down	26.25	222.00	11.00	2.75	120.75	5.50	203.00
Bow Up	26.45	7.50	1.50	0.75	65.00	52.00	60.25
Emerald Right	28.17	3.25	2.00	0.88	77.25	47.75	54.50
Victoria Up	36.07	193.75	5.75	1.63	136.50	5.50	250.75

Physical and chemical meltwater conditions varied with glacial influence (Table 2.3; Figure 2.2). Meltwater environments under high glacial influence were typically cold and turbid, had high TP, and low TN and specific conductivity relative to streams under low glacial influence (Figure 2.2). TDP, TDN, SRP, NO_2/NO_3, pH, and velocity were not related to glacier influence. Temperature ($p = 0.0092$, $r^2 = 0.59$) and specific conductivity ($p = 0.027$, $r^2 = 0.48$) were positively affected by decreasing glacial influence (Table 2.3; Figure 2.3). Turbidity significantly decreased with glacial influence ($p=0.0427$, $r^2 = 0.42$) (Table 2.3; Figure 2.3). Water chemistry parameters were not significantly affected by glacial influence.

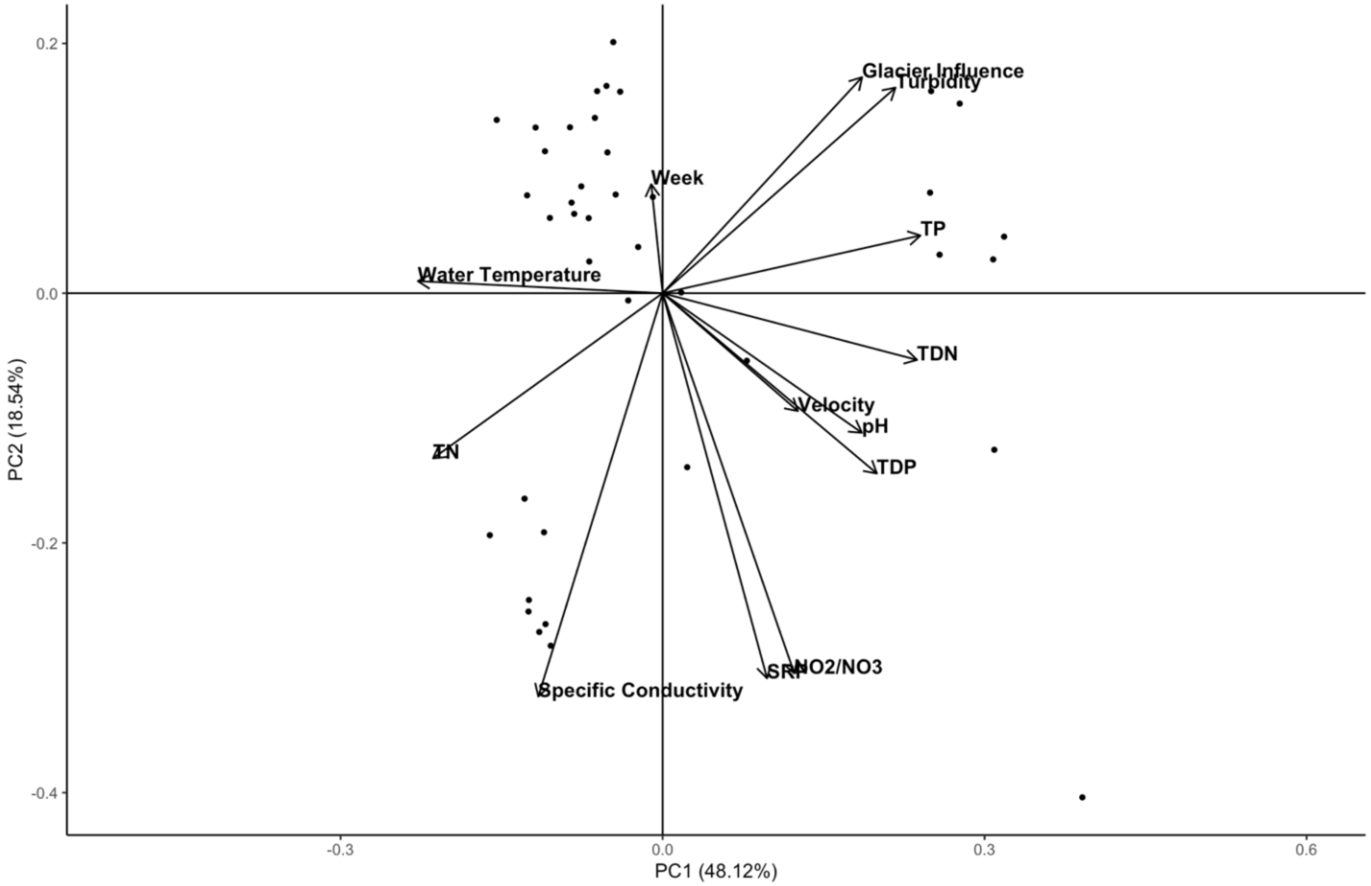
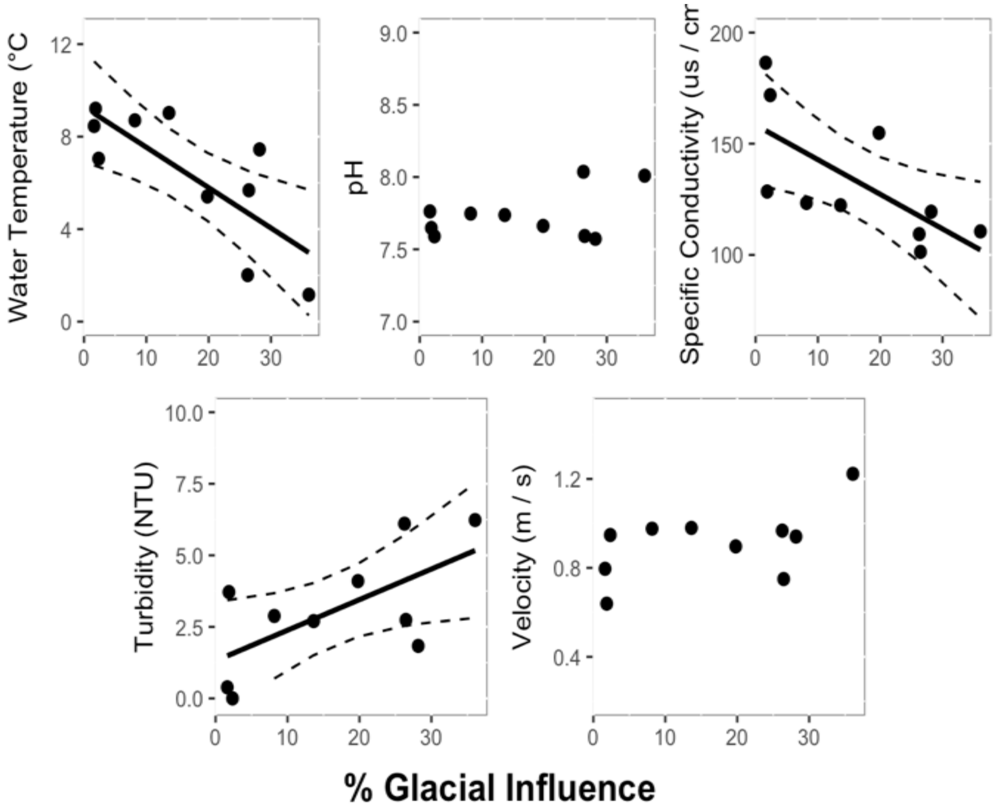


Figure 2.2. Principal component analysis of meltwater quality and chemistry parameters. All variables were scaled and centered prior to ordination.

a)


Water Temperature (°C
0
4
8
12
pH
7.0
7.5
8.0
8.5
9.0
Specific Conductivity (us / cm
100
150
200
Turbidity (NTU)
0.0
2.5
5.0
7.5
10.0
Velocity (m / s)
0.4
0.8
1.2
0
10
20
30
% Glacial Influence

b)

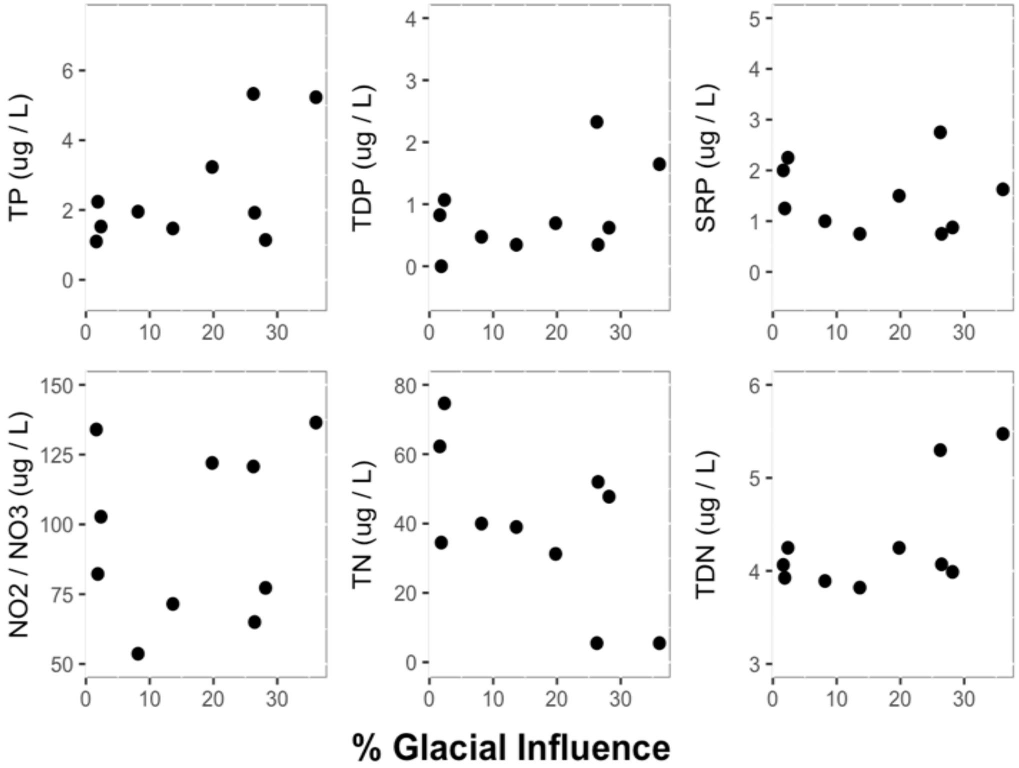

TP (ug / L)
0
2
4
6
TDP (ug / L)
0
1
2
3
4
SRP (ug / L)
0
1
2
3
4
5
NO2 / NO3 (ug / L)
50
75
100
125
150
TN (ug / L)
0
20
40
60
80
TDN (ug / L)
3
4
5
6
0
10
20
30
% Glacial Influence

Figure 2.3. Linear models of relationship between glacier influence and meltwater quality (a) and chemistry (b) variables. Statistically significant relationships are denoted using a trend line ($p < 0.05$). Dashed lines represent 95% confidence intervals. Turbidity, TP, TDP, and TDN were log-transformed prior to analysis.

Table 2.4. Summary statistics of linear regression models of the effect of glacier influence on meltwater quality and chemistry. Statistically significant relationships are bolded ($p < 0.05$).

Parameter	**F-statistic**	**p-value**	**r^2**
Water Temperature (°C)	**11.64**	**0.0092**	**0.59**
pH	1.54	0.25	0.16
Specific Conductivity (us/cm)	**7.28**	**0.027**	**0.48**
Turbidity (NTU)	**5.27**	**0.043**	**0.42**
Velocity (m/s)	3.36	0.1	0.30
TP (ug / L)	4.66	0.06	0.36
TDP (ug / L)	1.92	0.2	0.21
SRP (ug / L)	0.09	0.77	0.01
NO2 + NO3 (ug / L)	0.21	0.66	0.03
TN (ug / L)	5.13	0.053	0.39

3.2 - *Chl a-Environment Responses:*

Turbidity was a significant non-linear predictor of chl *a* concentration (GAM, edf = 3.23, F = 2.85; p = 0.04, while pH (F = 5.33, p = 0.03) and TDP (F = 4.84, p = 0.03) were significant linear predictors (Table 2.4). Glacial influence had a slightly positive effect on chl *a*, although this relationship was not statistically significant.

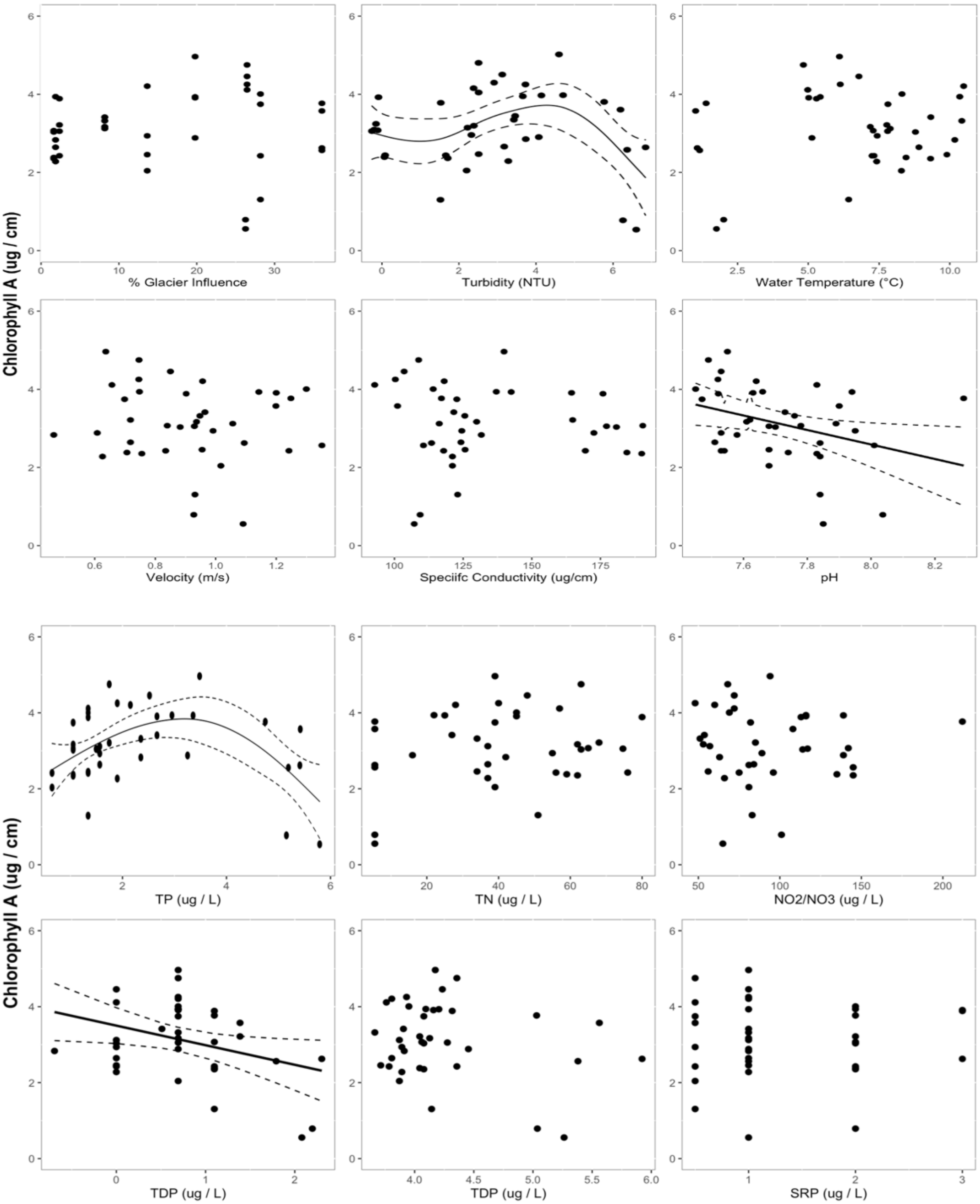


Figure 2.4. Effect of a) environmental and b) nutrient meltwater parameters on epilithic chl *a* concentration. Solid line indicates statistically significant predictors ($p < 0.05$). Dashed lines indicate 95% confidence intervals. Turbidity, TP, TDN, TN, TDP, and chlorophyll a were log-transformed prior to analysis. See Table 2.4 for model details.

Table 2.5. Model summary of relationship between environmental predictors and chl *a* concentration. Statistically significant relationships are bolded. AIC was used to determine model structure.

Parameter	F-statistic	p-value	r^2	Structure
Glacier Influence (%)	0.22	0.64	0.01	Linear
Turbidity (NTU)	**2.85**	**0.04**	**0.29**	**GAM**
Water Temperature (°C)	0.82	0.37	0.02	Linear
Velocity (m/s)	0.02	0.90	0.00	Linear
Specific Conductivity (us/cm)	0.13	0.73	0.00	Linear
pH	**5.33**	**0.03**	**0.13**	**Linear**
TP (ug / L)	**4.81**	**0.01**	**0.34**	**GAM**
TN (ug / L)	1.25	0.27	0.03	Linear
NO2 + NO3 (ug / L)	0.00	0.97	0.00	Linear
TDP (ug / L)	**4.84**	**0.03**	**0.12**	**Linear**
TDN (ug/L)	2.19	0.15	0.06	Linear
SRP (ug / L)	0.00	0.99	0.00	Linear

3.3 - *Epilithic Community Composition*

Taxonomically diagnostic algal pigments arranged in a unimodal pattern along the gradient of glacially influenced sites (Figure 2.5). Community composition was increasingly heterogeneous at sites with low glacial influence. Here, communities included greater abundances of diatoms, as represented by diadinoxanthin and diatoxanthin, and chlorophytes, represented by chl *b*. As glacial influence increased, the abundance of chlorophytes decreased, while the relative abundance of chrysophytes and diatoms (fucoxanthin) increased. Cyanobacteria (canthaxanthin, myxoxanthin, and zeaxanthin) were present at most sites, although in small abundances. Violaxanthin (chlorophytes) was present in low concentrations at most sites.

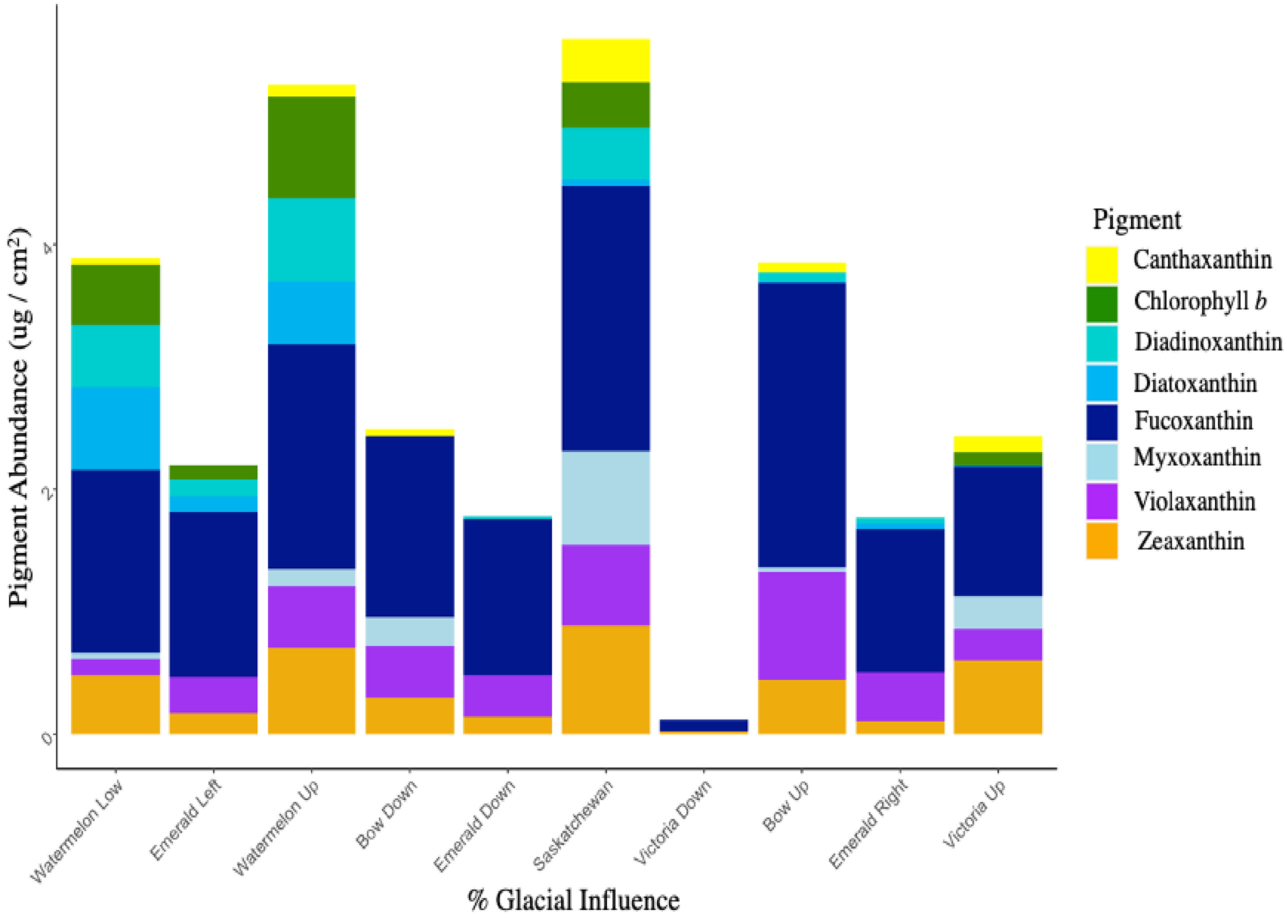


Figure 2.5. Mean diagnostic pigment abundances across an increasing gradient of glacial influence (left to right). Pigment data were log-transformed to down-weight the influence of rare pigments. Mean is representative of average pigment concentrations across five replicates, which were then averaged across four site visits in August 2022.

The composition of epilithic algal communities varied among sites and physio-chemical meltwater conditions. RDA was significant (*F*=1.96, *df*= 13, *p* = 0.002) capturing 52.0% of the variation in diagnostic pigment concentrations (Figure 2.6). Axis 1 was statistically significant (F= 18.6289, p= 0.001), explaining 30.9% of the total taxonomic variance. Axis 1 represented a glaciation gradient in which epilithon that contained relatively high concentrations of most algal pigments were contrasted from the more dilute communities that were collected from the more glacial streams. Here, forward selection identified specific conductivity as the only significant (*F*

= 10.415, $p < 0.001$) variable that explained the ordination of pigments and streams. Axis 2 separated cyanobacterial pigments (myxoxanthin, canthaxanthin and zeaxanthin) collected from more chemically concentrated streams from pigments affiliated with diatoms (fucoxanthin, diadinoxanthin, diatoxanthin) and chlorophytes (Chl *b*, violaxanthin), which were more common in epilithon under warmer stream conditions.

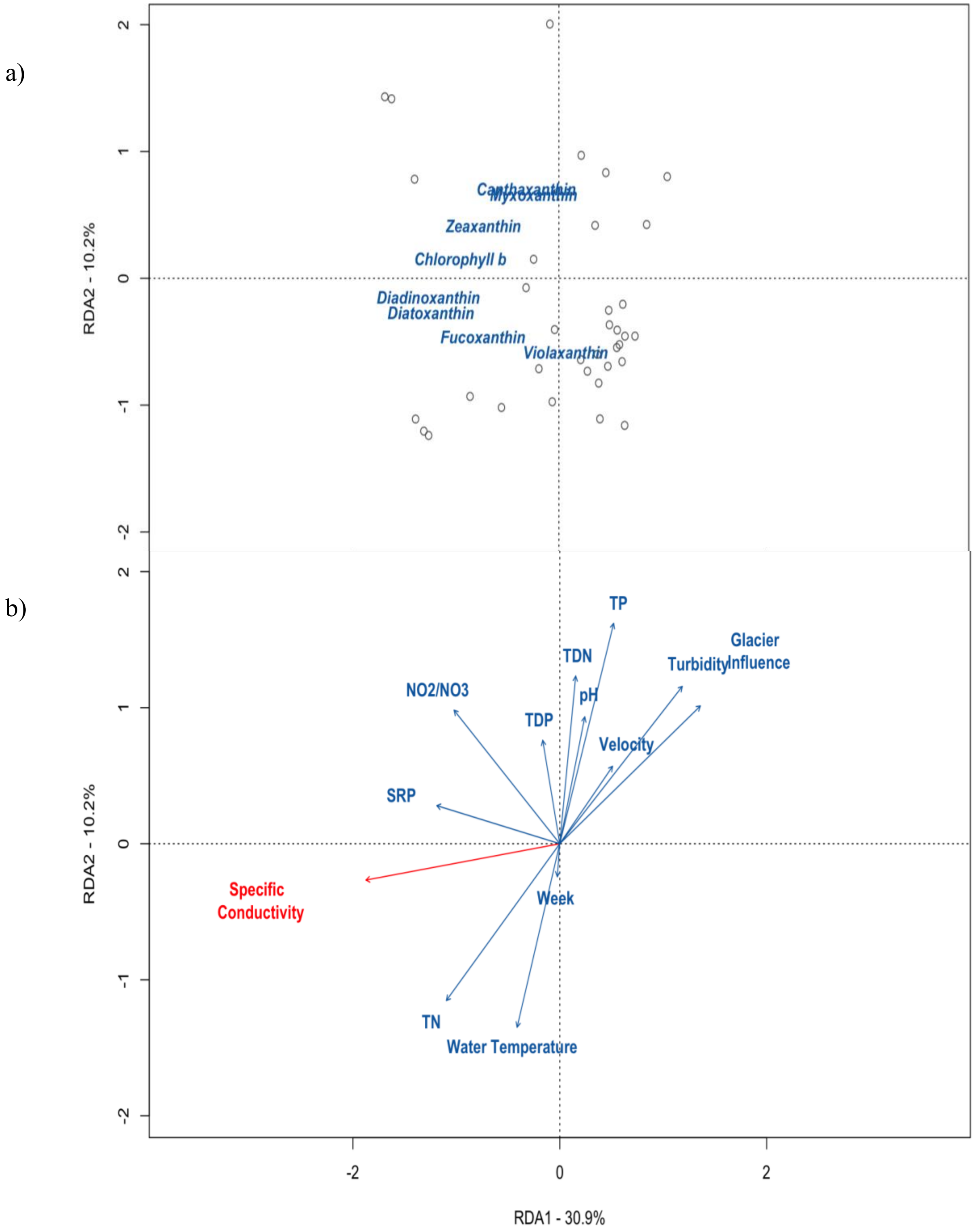


Figure 2.6. RDA triplot (scaling 2) of (a) diagnostic pigment concentrations constrained by (b) glacial meltwater quality and chemistry parameters. Statistically significant environmental predictors are displayed in red ($p < 0.05$). Turbidity, TP, TDN, TN, and TDP were log-transformed and all parameters were scaled and centered prior to analysis. Pigment data were Hellinger transformed to account for the high proportion of low pigment concentrations in certain sites (Legendre and Gallagher, 2001).

Discussion

This study generated novel findings regarding how epilithic algal communities in glacial streams may respond to further deglacialization during the 21st century. Instead of supporting my hypothesis of a negative relationship between epilithic algal biomass accrual and the extent of glacial influence within stream catchments, I discovered a unimodal relationship. Similarly, variation in epilithic algal community composition also appeared non-linear along the surveyed deglaciation gradient. These findings suggest that intermediate inputs of glacial meltwater function as subsidies to downstream ecosystems while declining or increasing amounts represent potential ecological stressors. Below, I provide possible explanations for my key findings.

Glacier loss alters meltwater conditions

Meltwater quality and chemistry sampled in this study largely adhered to abiotic templates of glacial streams described in the literature. Stream temperature significantly increased in streams with low glacial influence, although mean maximum temperatures were below 10°C for all sites throughout the study period (Figure 2.3; Table 2.3). Alpine stream temperatures are often correlated to glacial coverage, with near freezing meltwaters reflecting substantial glacial inputs (Brown et al., 2003; Brahney et al., 2021; Fellman et al., 2014). Specific conductivity also increased significantly with declining glacial influence (Figure 2.2; Table 2.3). High meltwater conductivity can be indicative of increased mineral-rich groundwater inputs, suggesting heterogenous water sources fed site within low glacial influence catchments, such as Watermelon Creek (Brown et al., 2003; Hood and Berner, 2009). Low turbidity was also significantly associated with declining glacial influence (Figure 2.2; Table 2.3). For example, the highest glacial influence site (Victoria Up) had turbidity values above 200 NTU, while turbidity remained below 2 NTU at the lowest glacial influence site (Watermelon Down). Glacial flour, a primary control of turbidity in glacial streams, is an erosional biproduct of glaciers grinding on bedrock below them (Hodson et al., 2004; Milner et al., 2017). The production and transport of this suspended sediment slows as glaciers retreat, shifting meltwaters towards increasingly clear states (Milner et al., 2017).

Water chemistry parameters did not significantly vary along the gradient of glacial influence. (Figure 2.2; Table 2.3) Elser et al., (2020) hypothesized that glacier loss will shift the supply of nitrogen and phosphorus to glacial streams, as increased inorganic and organic forms of nitrogen succeed dwindling SRP loads. Meltwater streams within heavily glaciated catchments typically have elevated phosphorus concentrations, due to phosphorus-sorbed sediment readily flushed from subglacial channels during melt seasons (Hodson et al., 2004). Although TP and TDP concentrations declined with decreasing glacial influence, these responses were primarily driven by extreme values within Victoria Creek, with concentrations varying little between remaining sites (Figure 2.2; Table 2.3). I also found no relationship between SRP and glacial influence, as mean concentrations were less than 3 ug / L across all sites (Figure 2.2; Table 2.3). It is possible that the relatively short gradient of glacier influence sampled in this study was not comprehensive enough to elicit the predicted SRP responses to glacier loss. However, several studies have similarly not found evidence of glacier coverage-SRP relationships (Fell et al., 2018; Rinke et al., 2001; Uehlinger et al., 2010; Warner et al., 2017). Given these oft conflicting patterns, I suggest caution when predicting how biologically available phosphorus responds to glacier loss and that regional differences in bedrock composition, subglacial flushing rates, and sorption strength should be considered when analyzing SRP trends (Hodson et al., 2004).

Glacial influence was not a strong predictor of meltwater nitrogen content. Increased nitrogen concentrations in alpine streams are indicative of mixing with non-glacial water sources (Hood and Berner, 2009). Low glacial influence sites did have greater TN concentrations (Figure 2.2; Table 2.3), and as these sites were also highly conductive, groundwater likely represents an important pool for TN within meltwater streams in my study region. Glacier loss can also decrease NO_2/NO_3 supply to North American meltwaters (Hood and Berner, 2009; Lafrenière and Sharp, 2005; Warner et al., 2017). However, NO_2/NO_3 concentrations were variable across sites in this study. Undeveloped soils within the study region due to increased rock and ice coverage could limit terrestrial inorganic nitrogen retention, thereby moderating its availability in low glacial influence sites (Lafrenière and Sharp, 2005).

Algal biomass responses to glacier loss

Glacier influence had a variable effect on chl *a*-inferred algal biomass (Figure 2.4). We hypothesized that lower glacial influence would produce greater biomass accrual due to decreased physical disturbance and greater light availability (Boix Canadell et al., 2021; Uehlinger et al., 2010). Instead, biomass was low in both high and low glacial influence streams relative to intermediate influence sites. The unimodal distribution was largely driven by increased diatom and chrysophyte abundance at moderate levels of glacial influence (Figure 2.5).

Both positive and non-linear algal biomass responses to declining meltwater harshness have previously been observed in deglaciating catchments globally (Cauvy-Fraunié et al., 2016; Khamis et al., 2016; Niedrist et al., 2018). However, the specific environmental conditions responsible for these biomass responses are rarely identified, limiting the development of mechanistic hypotheses regarding consequences for algal growth as glaciers disappear.

Declining meltwater turbidity and TP best explained the unimodal response of epilithic biomass to declining glacier influence (Figure 2.6; Table 2.4). Meltwater turbidity impacts algal biomass through two key processes: disturbance and light availability. Glacial flour and streambed instability act together to impose a frequent and intense physical disturbance regime that limits potential biomass accumulation through biofilm scouring and abrasion in glacial streams (Biggs et al., 1999b; Boix Canadell et al., 2021; Khamis et al., 2016; Uehlinger et al., 2010). As glaciers recede, scouring pressure subsides and clearer meltwaters increase light availability for epilithic algae. Aquatic environments in high elevation landscapes incur high intensities of photosynthetic active radiation (PAR) and ultraviolet radiation (UVR) compared to those downstream (Rose et al., 2014). Many epilithic algae in glacial streams are adapted to the dark benthic environments maintained by turbid meltwaters and require low light availability to accumulate biomass due to sensitive and efficient photosystems (Aigner et al., 2018; Martyniuk et al., 2014). For these communities, excessive light exposure in low turbidity meltwaters can inhibit growth through photoinhibition by damaging the photosynthetic machinery of species adapted to low light (Aigner et al., 2018; Boix Canadell et al., 2021; Martyniuk et al., 2014). For example, Aigner et al. (2018) showed that even moderate levels of PAR exposure could trigger photoinhibition in a colonial cyanobacteria commonly found in dark alpine waters. Overexposure to UVR also damage cells, further limiting benthic biomass accumulation (Vinebrooke and Leavitt, 1999). In tandem, photoinhibition and UV damage should inhibit epilithic biomass in increasingly clear glacial streams.

TP was also a strong predictor of epilithic biomass. Increased phosphorus loads can provide epilithic algae with nutrients crucial for cell growth in mountain streams otherwise within nutrient-limited landscapes (Elser et al., 2020; Wellnitz et al., 1996). However, meltwater TP is strongly influenced by suspended sediment loads in glacial streams as phosphorus is often bound to glacial flour (Hodson et al., 2004). Therefore, it is difficult to determine whether nutrient availability or disturbance is the primary mechanism driving the unimodal biomass responses observed in this study. As TP is not readily bioavailable, I attribute the observed unimodal biomass response to glacial influence on turbidity-driven disturbance regimes (Boix Canadell et al., 2021; Rinke et al., 2001). Support for this hypothesis comes from Rinke et al. (2001) who tested if algal growth was nutrient limited in glacial streams using nutrient diffusing substrata over a summer melt period. However, nutrient exposure explained little variation in biomass compared to flow-related predictors. I also found that environmental predictors involved in disturbance regimes superseded the low predictive power of bioavailable nutrient concentrations, such as NO_2/NO_3 and SRP. I expect that relatively low nutrient requirements in depauperate biofilms and increased mass transfer of nutrients into biofilms due to swift moving waters mitigate potential nutrient scarcity (Biggs et al., 1999). Nutrient availability may become of further importance as harsh glacial conditions cede to promote increased colonization (Elser et al., 2020; Robinson et al., 2002; Uehlinger et al., 2010).

Between these turbidity extremes, moderate glacial influence provides sustained opportunities for algae to accumulate biomass. Decreased streambed disturbances promotes increasingly diverse biofilms, including species with high biomass filamentous growth forms (Fell et al., 2018; Rott et al., 2006). Suspended glacial flour further benefits benthic biomass production through photoprotection. Here, suspended glacial sediment scatters PAR and UVR, decreasing the incidence of photoinhibition (Elser et al., 2020; Martyniuk et al., 2014; Rose et al., 2014). In fact, epilithic algae in clear meltwaters can rapidly accumulate biomass when exposed to pulses of pulses of turbid glacial inputs as photoinhibition lifts (Martyniuk et al., 2014). Lastly, moderate loads of glacial flour should provide biofilms with increased access to crucial bioavailable nutrients needed to growth, such as SRP (Elser et al., 2020; Rott et al., 2006).

Algal community responses to glacier loss

Epilithic algal community composition was affected by shifting meltwater conditions along a gradient of glacial influence. Epilithic biofilms subject to high glacial influence (i.e. cold, turbid, and fast moving waters) generally have low algal diversity and are composed primarily of specialized diatoms with resistance traits such as strong attachment abilities and small cell sizes (Rott et al., 2006; Fell et al., 2018; Gesierich and Rott 2012). My taxonomic pigment analysis revealed that diatom-related pigments were indeed present across all sites and composed a large proportion of communities within high glacial influence sites (Figure 2.5). However, communities these sites also included chrysophytes (i.e. *Hydrurus foetidus*) and colonial cyanobacteria (i.e. *Champaesiphon* spp.) (Figure 2.5). Likely, disturbance tolerance towards harsh meltwater environments is not only conveyed in specialized diatoms, but also to smallcelled, non-motile, and mucous-producing colonial species within other algal groups (Hieber et al., 2001; Rott et al., 2006).

I observed increasingly heterogeneous community composition as glacial influence decreased, supporting our first hypothesis (Figure 2.4; Figure 2.5). These communities included green algae which were absent in harsher meltwaters, along with increased abundances of diatoms and chrysophytes. Glacier loss should benefit the colonisation of species with filamentous growth forms, such as the chlorophytes *Ulothrix spp*. and *Klebsormidium spp*. (personal observation) identified in Watermelon Creek, due to decreased disturbances regimes as flows lessen and scouring pressure declines in clearer waters (Biggs et al., 1998; Hieber et al., 2001).

Individual meltwater habitat characteristic poorly explained algal community composition. Of the water quality parameters measured in this study, only specific conductivity significantly explained variation in epilithic community structure (Figure 2.4). Groundwater contributions associated with increased ionic strength have often weaker disturbance regimes than glacial flows along with water temperatures and clearer waters, characteristics that should benefit increased colonization of algal species with diverse life-history traits (Brown et al., 2003; Fell et al., 2018; Hood and Berner, 2009; Niedrist et al., 2018; Rott et al., 2006; Smith et al., 2001). Although turbidity and velocity were not statistically significant predictors of epilithic community composition here, disturbance-related meltwater conditions have previously been reported as important filters for diatom biodiversity and function in glacial streams (Fell et al., 2018). Indeed, decreased meltwater turbidity and velocity were associated with greater abundances of diatom-related pigments across our study sites (Figure 2.4). As waters slow, decreased shear stress and streambed instability facilitate the colonization of diatom species with diverse growth forms (Biggs et al., 1998). For example, Wellnitz and Rader (2003) observed in their study of periphyton in subalpine Rocky Mountain streams that algal communities exposed to scouring from high flows were primarily composed of tightly attached species with streamlined growth forms, such as *Hydrurus foetidus*. The same communities, when placed into a nearby stable side channel with low streambed transport, expanded to contain species with diverse growth forms. Continued glacier loss should further reduce turbidity, streambed movement, and velocity intensity to increase epilithic algal community diversity in glacial streams.

Meltwater chemistry parameters were poor predictors of epilithic community composition. Low SRP and DOC availability across all sites included in this study indicate that nutrient availability may be of secondary importance for the structure of epilithic biofilms compared to disturbance-related conditions (Boix Canadell et al., 2021; Rinke et al., 2001). SRP varied little along our gradient of glacial influence and often approached or fell below its limit of detection while DOC fell below its detection limit in most sites (Figure 2.2; Table 2.3). Despite its low concentrations, SRP is critical to maintaining quick algal growth rates necessary to contend with rapidly changing glacial stream environments (Elser et al., 2020; Rott et al., 2006). To combat nitrogen and phosphorus scarcity in glacial streams, epilithic algae rely on a variety of nutrient capture strategies (Rott et al., 2006). Traits such as phosphatase-synthesizing hairs and nitrogen-fixing heterocytes can help mitigate nutrient scarcity by increasing capture efficiency (Rott et al., 2006). Algae also exchange nutrients with other microbiota within epilithic biofilms in to acquire essential nutrients during periods when other meltwater conditions are conducive to epilithic growth (Busi et al., 2022). I hypothesize that although nutrient supply may promote the establishment of diverse biofilms as competition for resources increases, physical disturbance is a stronger filter of epilithic diversity; an order of operations also shown to control primary productivity in glacial streams (Boix Canadell et al., 2021; Rinke et al., 2001).

Conclusion:

Environmental heterogeneity created by moderate glacial influence is crucial to maintaining diverse and productive meltwater ecosystems. Previous research has identified that glacial influence can positively affect benthic algal and macroinvertebrate beta-diversity, species richness, density, and biomass (Brown et al., 2007; Fell et al., 2018; Jacobsen et al., 2012; Khamis et al., 2016; Niedrist et al., 2016). Glacial melt inputs are hypothesized to create a matrix of streambed habitat conditions that moderate competitive stress from downstream colonizers while also maintaining habitat requirements for glacial meltwater specialists (Jacobsen et al., 2012; Khamis et al., 2016; Milner et al., 2017). However, glacier loss ultimately homogenizes meltwater environments so that conditions previously critical to producing spatially and temporally diverse benthic habitats increasingly resemble slower, warmer, and clearer downstream environments (Brown et al., 2003; Milner et al., 2017). These abiotic transitions, although associated with increased recruitment of downstream generalists, should further stress glacial stream ecosystems with potential consequences for meltwater ecosystem function.

Lower epilithic biomass in clear meltwater streams as glaciers disappear could have consequences for the productive capacity of glacial streams. Glacial stream food webs rely on epilithic algae for an energetic base in otherwise energy-sparse landscapes (Niedrist et al., 2016; Busi et al., 2022; Zah et al., 2001). Here, I show that rapidly melting glaciers threaten to constrain algal biomass due to declining meltwater turbidity. Recent interest in the potential for glacier loss to create habitat for downstream species currently experiencing stress due to climate change places further importance on the development of food resources in glacial streams (Bellmore et al., 2022; Fellman et al., 2015; Pitman et al., 2021; Schoen et al., 2017). For example, glacier loss is expected to create over 6000 km of viable pacific salmon stream habitat along the west coast of Canada and the United States (Pitman et al., 2021). While slower flows, warmer temperatures, and stable streambeds should indeed benefit the colonization of downstream species currently faced with declining habitat, decreased meltwater harshness are but a part of successful habitat creation. Successful upstream colonization also requires adequate food resources (Bellmore et al., 2022). The results suggest that glacier loss could increasingly constrain food availability for higher trophic levels due to increased photoinhibition of epilithic algal growth. Further research is now needed to mechanistically quantify how ice loss impacts algal growth and its potential consequences for trophic energy transfer as glaciers continue to disappear.

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Chapter 3: Effects of glacial flour on epilithic algal communities in mountain streams: a mesocosm experiment

Introduction:

Alpine streams fed by glacial meltwater are experiencing rapid environmental changes as glaciers disappear from mountain regions globally (Milner et al., 2017). The turbid, frigid and fast flowing meltwaters that define the harsh conditions of these streams are products of natural glacial melt processes (Brown et al., 2003). However, accelerated glacier loss has mediated many of these previously extreme environments to resemble those of less harsh snowmelt and groundwater sources (Brahney et al., 2021; Milner et al., 2017). Here, relative increases in the contribution of non-glacial sources due to decreased meltwater production are predicted to produce less turbid, warmer and slower flowing lotic conditions (Milner et al., 2017; Sudlow et al., 2023).

Epilithic algal communities are indicative of shifting habitat conditions in glacial meltwater streams. For example, less glacial influence promotes diatom diversity as “windows of opportunity” for algal growth become more common during the autumn (Fell et al., 2018; Hieber et al., 2001; Uehlinger et al., 2010). However, although trends in epilithic algal abundance and community composition are well-described in meltwater streams as glaciers recede, it remains challenging to identify the importance of the various ecological drivers. Conceptual frameworks developed for macroinvertebrate diversity based on stream temperature and channel stability provide a template for establishing mechanistic hypotheses focused on epilithic primary producers (Milner et al., 2001). For instance, while only cold-adapted macroinvertebrates are present in streams below 2°C, progressively warmer temperatures promote the establishment of species with more diverse life histories and variable thermal tolerances (Milner et al., 2001). The crucial role of epilithic algae as the energetic base of lotic food webs in glacial meltwaters behoves a similar detailed approach as loss of glaciers threatens to alter the habitat conditions to which they are adapted (Niedrist et al., 2018).

Turbidity is critical to the structure of epilithic algal communities in glacial meltwater streams (Rott et al., 2006; Sudlow et al., 2023). Turbid glacial flows result from high loads of suspended “glacial flour”, a fine sediment produced by the erosion of bedrock beneath glaciers (Hodson et al., 2004). When mobilized downstream, glacial flour is thought to affect epilithic algae through two primary mechanisms: physical disturbance and attenuation of solar irradiance. Highly turbid streams can damage biofilms through frequent and intense scouring (Boix Canadell et al., 2021; Rott et al., 2006; Sudlow et al., 2023). These disturbances are expected to exert a strong effect on algal diversity and growth, limiting communities to species with strong attachment abilities and streamlined growth forms (Rott et al., 2006). Glacial flour also diminishes underwater light availability to epilithic algae by effectively scattering incoming photosynthetic active radiation (PAR) and ultraviolet radiation (UVR) (Boix Canadell et al., 2021; Rose et al., 2014). To contend with low light availability, species found in glacial streams often have efficient photosystems and minimal light requirements for photosynthesis (Aigner et al., 2018; Martyinik et al., 2014). However, widespread and rapid glacier loss is decreasing the supply of glacial flour downstream, creating clearer waters with less suspended sediment (Elser et al., 2020; Hood and Berner, 2009; Milner et al., 2017; Sudlow et al., 2023). Lower meltwater turbidity subjects epilithic communities to reduced disturbance frequencies and intensities while also exposing streambeds to greater light intensities (Boix Canadell et al., 2021; Fell et al., 2018). While decreased disturbance should benefit the colonization of species with larger growth forms and promote increased biomass (Rott et al., 2006; Uehlinger et al., 2010), the consequences of increased light availability are less clear. Greater light exposure highlight can both benefit (Boix Canadell et al., 2021) and depress algal growth in glacial streams (Boix Canadell et al., 2021; Martyniuk et al., 2014; Martyniuk et al., 2019), as well as decrease the nutritional quality of algae for consumers (Martyniuk et al., 2019). Here, increased potential for photosynthesis is likely antagonized by detrimental photoinhibition as algal species adapted to previously shaded environments lack the capacity to tolerate intense light (Ainger et al., 2018; Martyniuk et al., 2014; Rott et al., 2006). However, little is known whether meltwater turbidity elicits net positive or negative epilithic algal growth responses.

Creative experimental approaches can provide the explanatory power needed to identify the mechanisms responsible for the ecological consequences of rapidly changing meltwater environments (Hotaling et al., 2017). For primary producers in meltwater streams, the effects of glacier loss are mainly characterized indirectly through space-for-time substitutions and glacial influence gradients (Cauvy-Fraunié et al., 2016; Fell et al., 2018; Gesierich and Rott, 2012; Khamis et al., 2016; Niedrist et al., 2018). While these studies provide novel insights into how glacier loss alters algal biodiversity and biomass, hypothesized mechanisms driving these community responses remain relatively untested. However, a few recent experiments have advanced our understanding of primary producers in glacial streams (Cauvy-Fraunié et al., 2016; Martyniuk et al., 2014; Martyniuk et al., 2019). For example, shading experiments over clear glacial streams in Patagonia showed how excessive light exposure can suppress algal growth, contrary to previous hypotheses (Martyniuk et al., 2014; Martyniuk et al., 2019). Future experiments directly testing how ameliorating abiotic conditions impact primary producers should further benefit our knowledge of how glacial stream ecosystems will change as ice increasingly disappears from alpine landscapes.

Using a series of stream mesocosms in a controlled environment, we test how five levels of meltwater turbidity affects algal communities from glacial streams. We hypothesize that communities exposed to moderate turbidity meltwater will have greater biomass than in low turbidity streams as algae are relieved from photoinhibition (Aigner et al., 2018; Boix Canadell et al., 2021; Martyniuk et al., 2014; Martyniuk et al., 2019). Here, glacial flour attenuates incoming light, creating low-light environments that benefit algae adapted to otherwise extremely low light conditions in turbid glacial streams (Rose et al., 2014). We also expect that extreme turbidity will subsequently decrease algal biomass relative to intermediate levels due to increased physical disturbance in the form of scouring or sedimentation (Boix Canadell et al., 2021; Rott et al., 2006; Uelinger et al., 2010). Finally, diatoms and other chromophytes are expected to drive changes in total community biomass as they represent the major taxonomic group reported in surveys of epilithon in glacial streams (Hieber et al., 2001; Niedrist et al., 2018). By experimentally testing how glacial stream turbidity alters algal growth, we hope to further quantify the consequences of decreasing meltwater turbidity due to rapid glacier loss on alpine stream ecosystems.

Methods:

Sample Collection

We collected epilithon and meltwater from Watermelon Creek, a clear glacier-fed stream in Banff National Park, Canada (Table 3.1.; Figure 3.1). Mixed forest, rock, and snow/ice cover are the primary landcover types within Watermelon Creek watershed. Bankside vegetation surrounding our sampling site is predominantly grass and shrubs, with conifer trees present further inland.

Figure 3.1. Watermelon Creek (left) and Victoria Creek (right), in Banff National Park, Canada. Photo credit: Karson Sudlow.

Table 3.1. Site characteristics of Watermelon Creek and Victoria Creek. Temperature and turbidity measurements were measured weekly in August 2023 using a YSI Exo2 Sonde (n=4).

Site	**Watermelon Creek**	**Victoria Creek**
Location	51.6669, -116.31178	51.3947, -116.31178
Elevation (m)	1984	1911
Mean August Temperature (°C)	8.46	2.01
Mean August Turbidity (NTU)	2.14	491.59
% Glacier Coverage	1.6	26.3

To collect epilithon, we randomly placed 100 5 x 10 cm unglazed terra cotta tiles along an unshaded reach of Watermelon Creek in September 2023. Harsh meltwater conditions, such as high discharges and turbidity, wane in fall as glacial melt rates slow, creating a “window of opportunity” suitable for collecting algal biofilms (Uehlinger et al., 2010). Tiles were incubated for three weeks to allow for the development of epilithon. We then transported colonized tiles to the University of Alberta by placing them in sealed bags filled with stream water as to not disturb biofilms. We also collected stream water from Watermelon Creek for our experimental streams by filling 40 litre carboys at a downstream location from our incubation site. Additional water samples were collected twice in October 2023.

We gathered glacier flour from deposits on the banks of Victoria Glacier Creek to create our turbidity treatments (Table 3.1.; Figure 3.1.). This stream is by a large glacier that supplies large amounts of glacial flour downstream. Using a shovel, we collected approximately 10 kg of glacial flour and other fine sediments from recently formed deposits along stream edges. These deposits were made accessible due to declining stream discharges as glacier melt slowed into fall. Glacial flour was transported back to the University of Alberta, put into enamel trays, and dried at room temperature for 48 hours.

Stream Mesocosms

The experiment took place at the University of Alberta in a controlled artificial growth chamber. We set the ambient chamber temperature to 11°C to replicate cold environment found in alpine environments. The chamber was lit by 30 Philips 86-Watt fluorescents arranged across the ceiling in a parallel row. Light was available for 16 hours a day, from 6 A.M. to 10 P.M. We constructed 20 artificial stream channels using six-mm thick clear plexiglass and water resistant silicone (Figure 3.2.). Each channel measured one metre long and 15 cm wide, with a back plate and two side walls all 7.5 cm tall. Stream channels then sat on a metre high metal platform with each channel head raised 15 cm higher than its outflow to replicate a downwards slope. Five treatment groups each consisting of four mesocosms were separately fed by water from a 40-L plastic reservoir placed below the metal platform. In each reservoir, a 3000-L per hour submersible pond pump fed water through metre long plastic tubing to input valves at the head of each stream channel. Five plastic containers were placed below each group of four streams to recycle flow back into its corresponding reservoir (Figure 3.1).

Figure 3.2. Left – Artificial stream mesocosms in a controlled growth chamber at the University of Alberta. Right – Experimental set-up with five unglazed terra cotta tiles colonized by epilithic algae placed into each of 20 stream channels.

Prior to the experiment, reservoirs were filled with 20 litres of clear glacial meltwater. Five colonized tiles were then placed into each stream channel and left to acclimate to the experimental environment for two weeks (Figure 3.2.). After this two-week incubation period, we inoculated each reservoir with varying amounts of glacial flour to create five turbidity treatments including a control with each treatment replicated four times. Treatments were as follows: a control with no glacial flour added, and low, moderate, high, and extreme turbidity treatments averaging 1.15, 5.10, 30.17, 105.48, and 247.62 NTU, respectively (Table. 3.2). Each treatment level was achieved by incrementally adding 10 grams of glacial flour to each reservoir, monitoring turbidity with a YSI Exo2 Sonde fitted with a turbidity probe. Treatment levels were chosen to be representative of turbidity measured in glacial streams across the Canadian Rockies (see Chapter 2). To prevent the sedimentation of glacial flour onto basin bottoms, we agitated the contents of each reservoir twice per day, once in the morning and once at night, by stirring with a large, graduated cylinder.

Table 3.2. Summary of experimental turbidity treatments and the approximate % glacial influence each represents (see chapter 2).

Treatment Level	**Average Turbidity (NTU)**	**% Glacial Influence**
Control	1.15	1
Low	5.1	3
Intermediate	30.17	10
High	105.48	20
Extreme	247.62	35

Data Collection

We harvested epilithon for each of the mesocosms on a weekly basis to measure the abundance of major algal groups and total community biomass over a five-week period. At the beginning of each week, we removed one tile per stream channel and scrubbed a 5 x 10 cm area for 30 seconds using an electric toothbrush. Tiles, the toothbrush head, and any algal residue were then rinsed into an enamel pan with 50ml of deionized water to form an algal slurry. To concentrate the harvested algae, we filtered each slurry through a 0.45um Whatman filter using a filter tower and hand pump. Filters were then placed into petri dishes and stored in a -20 °C freezer. All equipment was thoroughly rinsed with deionized water between samples. After sampling, tiles were placed back into their original position within each channel. The following week, a previously unsampled tile was randomly chosen for sampling. This continued for five weeks until all tiles per channel were harvested for epilithon.

We also monitored the water chemistry of each reservoir once per week throughout the experiment. For each reservoir, we measured turbidity, water temperature, pH, dissolved oxygen, and specific conductivity using a YSI Exo2 Sonde. A 50 mL unfiltered water sample was collected from each reservoir and stored at 4°C to measure total phosphorus (TP) and total nitrogen (TN). Another 50 mL of stream water was filtered through Whatman 0.45um cellulose acetate syringe filters to measure total dissolved nitrogen (TDN) and total dissolved phosphorus (TDP). These were also stored at 4°C.

Laboratory Analysis

Frozen algal pigment samples were prepared and analyzed by High Performance Liquid Chromatography following the procedures outlined in Cook et al. (2023). Pigment concentrations were reported as µg/cm2. Chlorophyll a (chl a) was used as a proxy for total algal biomass. Taxonomically diagnostic pigments, mainly fucoxanthin, diatoxanthin, diadinoxanthin, violaxanthin, zeaxanthin, and chlorophyll b, were used to infer the relative abundance of major algal groups according to Wright et al. (2005) (Table 3.3.).

Table 3.3. Diagnostic pigments and their corresponding algal groups. Chromophytes are represented by chrysophytes and diatoms.

Pigment	Algal group
Chlorophyll *a*	Total biomass
Chlorophyll *b*	Chlorophytes
Diadinoxanthin	Chromophytes
Diatoxanthin	Diatoms
Fucoxanthin	Chromophytes
Zeaxanthin	Cyanobacteria
Violaxanthin	Chlorophytes

Water chemistry analysis was completed at the Biogeochemical Analytical Services Laboratory at the University of Alberta. TN, TDN, TP, and TDP were analyzed using a Lachat QuikChem 8500 FIA Automated Ion Analyzer.

Statistical Analysis

Prior to analyses, chlorophyll concentrations were assessed for extreme outliers using box plots (Figure 3.3). No extreme outliers were identified. Mean chl a and other pigment concentrations were calculated each week across replicates (n =4). A repeated-measure ANOVA was used to assess the statistical significance of turbidity, time, and their interaction, across the duration of the experiment at an alpha level of 0.05. This test is robust to violations of normality (Blanca et al., 2023). We then used a post-hoc pairwise t-test with Bonferroni-adjusted p-values to identify statistically significant treatment levels for each week of sampling. To assess if turbidity, time, and their interaction impacted community composition as inferred by diagnostic pigment concentrations, we used a repeated-measures MANOVA using a parametric bootstrapping approach with 1000 iterations. This approach iteratively tests heteroscadastic singular covariance matrixes which violate the assumptions of a typical MANOVA model (Friedrich and Pauly, 2018). All statistical analysis was performed in R Studio version 2021.09.1 (Oksanen et al., 2020). The repeated measures MANOVA was performed using the MANOVA.RM package (Friedrich et al., 2022).

Results:

Physio-chemical meltwater conditions

Meltwater temperature, pH, and dissolved oxygen within each basin were similar across treatment levels, except for specific conductivity which was highest for the extreme turbidity treatment (Table 3.4.). Mean water temperature varied between 10 and 11°C across treatments and weeks. All reservoirs also maintained a slightly basic pH of approximately 8. Dissolved oxygen was relatively similar between treatments and increased from approximately 90% to 92% over the duration of the experiment. TP increased with turbidity, though the high treatment had slightly greater mean TP concentrations (169 µg/L) than the extreme treatment (96.8 µg / L). Intermediate and high treatments had increased TDP (41.4 µg / L and 60.8 µg / L, respectively) compared to < 15 µg/L for control, low, and extreme treatments. TN and TDN were relatively low for intermediate and high treatments (451.4 µg/L and 406.6 µg/L, respectively) compared to control (1201.6 µg/L), low (1195.4 µg/L), and extreme treatments (2064 µg/L).

Table 3.4. Mean meltwater quality and nutrient conditions for control, low, intermediate, high, and extreme turbidity treatments. Meltwater quality (temperature, pH, and dissolved oxygen) were measured every week for five weeks using a YSI Exo2 Sonde. Values reflect data collected during the first four weeks of the experiment due to instrument error during week (n = 4). Meltwater chemistry (TP, TDP, TN, and TDN) and specific conductivity were measured every week for five weeks (n = 5).

Treatment	Temperature (°C)	pH	Dissolved Oxygen (%)	Specific Conductivity (µS/cm)	TP (µg / L)	TDP (µg / L)	TN (µg / L)	TDN (µg / L)
Control	10.69	8.14	91.25	509.6	21	13.2	1461.8	1201.6
Low	11.09	8.15	91.40	506.8	15.2	5.25	1314	1195.4
Intermediate	11.26	8.13	91.76	495.2	85.2	41.4	705	451.4
High	11.67	8.13	91.23	482.4	169	60.8	808.2	406.6
Extreme	11.08	8.11	91.10	585.8	96.8	4.8	2220	2064

Epilithic biomass

Epilithic chl *a* concentrations were highest in the intermediate and high turbidity treatments, while the control, low, and extreme treatments resulted in low concentrations throughout the experiment (Figure 3.3). For the intermediate treatment, mean chl *a* peaked in week 4, however concentrations were highly variable across replicates. Mean chl *a* peaked in week 3 for the high treatment (Figure 3.3.). Turbidity had a statistically significant effect on chl *a* ($F_{(4,12)} = 28.64$, $p < 0.001$; Table 3.4.; Figure 3.3.). Chl *a* concentration was also significantly affected by week ($F_{(4,12)}=3.855$, $p = 0.0307$). Lastly, the interaction between turbidity and week was statistically significant ($F_{(16, 48)} = 2.482$, $p = 0.00778$). Pairwise comparisons of turbidity treatments taken each week indicated that the concentration of chl *a* in the intermediate turbidity treatment was significantly greater than in the control, low, and extreme turbidity treatments on week 2 (RM-ANOVA; df = 4, p = 0.005, 0.008, 0.005, respectively; Table 3.6.) and week 3 (RM-ANOVA; df = 4, p = 0.012, 0.021, 0.014, respectively; Table 3.6.). Chl *a* was also greater in the high turbidity treatment compared to the control, low, and extreme treatments in week four and five, however these differences were not statistically different (Figure 3.3; Table 3.6.).

Table 3.5. Summery statistics of repeated measures ANOVA on the effects of turbidity, week, and their interaction on epilithic chl *a* concentration. Each treatment was replicated four times (n = 4).

Effect	Between Group Df	Within Group Df	F-Statistic	p
Turbidity	4	12	28.643	< 0.001
Week	4	12	3.855	0.031
Interaction	16	48	2.482	0.0078

Table 3.6. Summary statistics for pairwise paired t-test of turbidity treatments on epilithic chl *a* concentration per week. Adjusted p-values reflect a Bonferroni correction for multiple comparisons. Statistically significant differences (adjusted-p < 0.05) are identified in bold.

Week	**Group 1**	**Group 2**	**Statistic**	**Df**	**p-value**	**Adjusted p-value**
1						Not significant
2	**Control**	**Intermediate**	**-16.908**	**3**	**0.000451**	**0.005**
	Low	**Intermediate**	**-13.788**	**3**	**0.000826**	**0.008**
	Intermediate	**Extreme**	**16.3219**	**3**	**0.0005**	**0.005**
3	**Control**	**Intermediate**	**-12.261**	**3**	**0.001**	**0.012**
	Low	**Intermediate**	**-10.057**	**3**	**0.002**	**0.021**
	Intermediate	**Extreme**	**11.5863**	**3**	**0.001**	**0.014**
4						Not significant
5						Not significant

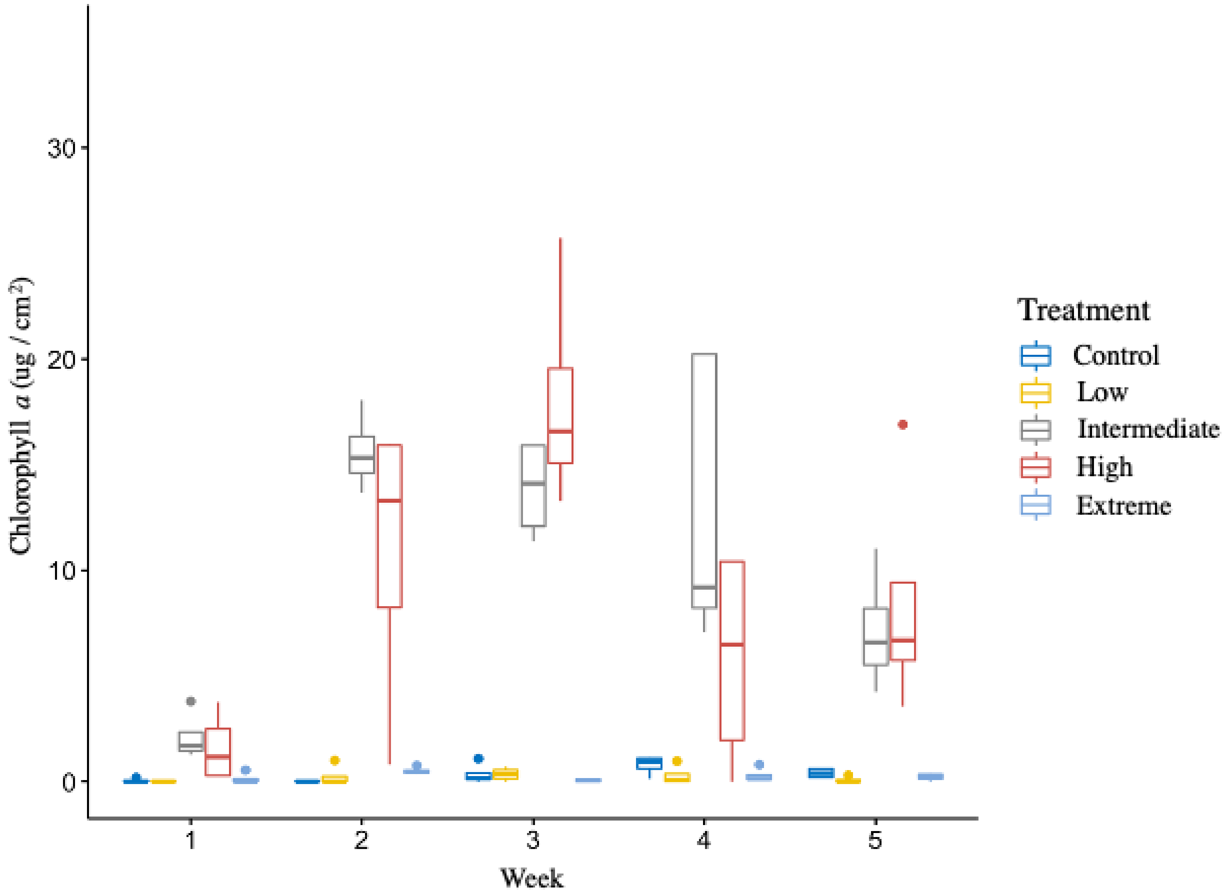

Figure 3.3. Box plot of epilithic chl *a* response to five meltwater turbidity treatments over five weeks (n = 5). Error bars represent 95% confidence intervals. Boxes represent the 75th quantile, median, and 25th quantile, from top to bottom.

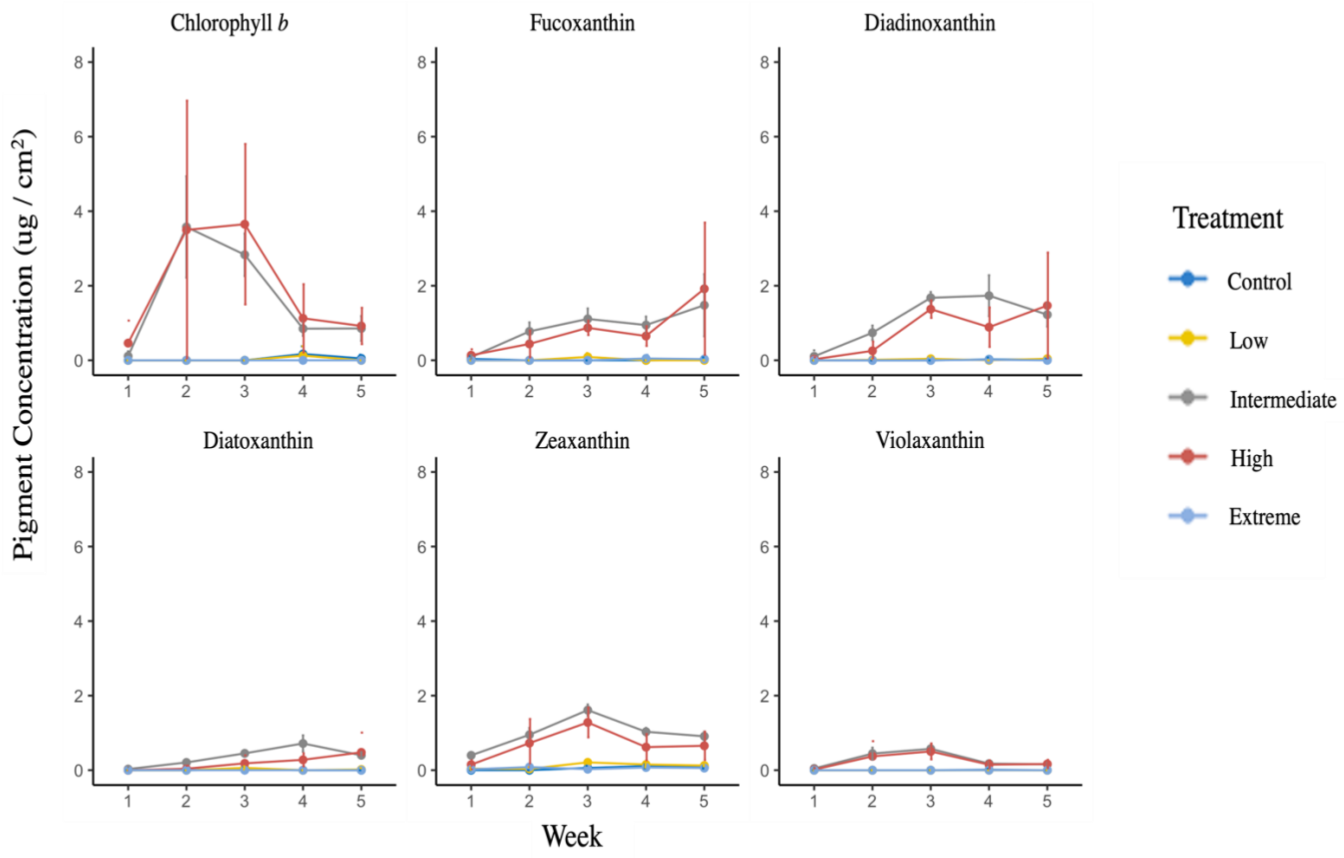

Figure 3.4. Mean taxonomic pigment concentrations in epilithic algal communities exposed to five turbidity treatments for five weeks. Error bars represent one standard deviation from the mean (n=4).

Table 3.7. Summery statistics of repeated measures MANOVA on the effects of turbidity, week, and their interaction on epilithic community abundance. Chl *b*, fucoxanthin, diadinoxanthin, diatoxanthin, zeaxanthin, and violaxanthin were used as proxies to measure the abundances of algal groups. Each treatment was replicated four times (n = 4). Test statistic generated using a parametric bootstrapping approach with 1000 iterations.

Effect	Test Statistic	p-value
Turbidity	1916.347	< 0.001
Week	864.088	< 0.001
Interaction	1290.227	0.003

Epilithic community composition

Turbidity had a significant effect on community composition (RM-MANOVA; Test Statistic = 1916.347; p < 0.001; Table 3.7). Algal community composition was also significantly affected by week (RM-MANOVA; Test Statistic = 964.088; $p < 0.001$; Table 3.7). Lastly, the interaction between week and turbidity had a statistically significant effect on community composition (RM-MANOVA; Test Statistic = 1290.227; p= 0.003; Table 3.7). Epilithic communities in the intermediate and extreme turbidity treatments were largely composed of chlorophytes during weeks 2 and 3 as identified by high concentrations of chl *b*, before declining in week 4 (Figure 3.4.). Chlorophytes were largely absent in the control, low, and extreme turbidity treatments. Intermediate and high turbidity treatments also stimulated chromophytes as evidenced by elevated concentrations of their pigments fucoxanthin and diatoxanthin (Figure 3.4.). Here, chromophytic pigment concentrations continued to increase throughout the experiment. The control, low, and extreme turbidity treatments had low concentrations of all indicator pigments.

Discussion

Meltwater streams have become increasingly clear as inputs of suspended sediment and discharges wane following glacier retreat (Milner et al., 2017). How these environmental changes impact these unique ecosystems under a rapidly changing climate remains a notable scientific knowledge gap, particularly in the case of the response of primary producers. Here, we provided novel experimental evidence that intermediate levels of glacial flour input foster increased epilithic algal biomass accrual. Further, stimulation of chlorophytes followed by diatoms supported the positive community-level response of epilithic algae to moderate levels of glacial turbidity. Below, we explore potential explanations for our key findings, which focus on the roles of intense physical disturbance under high glacial flour loading versus photo-inhibition and nutrient limitation under low turbidity conditions.

Turbidity impacts on epilithic biomass

High to extreme turbidity likely represented an intense physical disturbance, which significantly suppressed algal biomass accrual during the experiment. Here, the visible particulate size fraction of the glacial flour (i.e. silt) amendments was consistently observed tumbling down through the stream channels. Therefore, it is possible that intense scouring initially removed some of the established epilithon and then negated further algal development during the experiment, especially given the absence of physical refugia amongst the flat tiles. In addition, high turbidity also favours epilithic communities composed of small and compact algal growth forms that are better suited to withstand abrasion at the cost of not being very productive (Biggs et al., 1998; Francouer and Biggs, 2006; Rott et al., 2006). Scouring does appear to be the key mechanism by which high turbidity suppresses algal growth in glacial streams (Boix Canadell et al., 2021; Uehlinger et al., 2010; Vincent et al., 1986). For example, Boix Canadell et al. (2021) reported that above a threshold of streambed movement and scouring, algal productivity in glacial streams was increasingly determined by disturbance, while below this threshold, growth was primarily affected by light availability. Elsewhere, high loading of other types of suspended sediment can also damage or detach biofilms from substates, thereby reducing periphytic biomass (Biggs et al., 1998; Francouer and Biggs, 2006; Luce et al., 2012). Although high turbidity can also equate to reduced light availability and light limitation of epilithic algal growth (Boix Canadell et al., 2021), this was likely not a factor in our high turbidity treatments as light attenuation would have been minimal given the shallow depth (< 1 cm) of the water column streaming above the tiles.

Control and low turbidity treatments resulted in decreased algal biomass. Glacial flour is a key source of phosphorus in glacial streams and provides benthic organisms with nutrients needed to fuel rapid growth rates in streams with otherwise limited growing opportunities (Elser et al., 2020; Hodson et al., 2004). Indeed, mesocosms inoculated with less glacial flour had lower TP concentrations than treatments with increased turbidity. We expect that phosphorus scarcity limited biomass accrual as biofilms may have lacked the nutrients needed to sustain meaningful growth (Elser et al., 2020). While algae are resilient to low nutrient availability in glacial streams, nutrient diffusion experiments suggest that phosphorus limitation has important influence on biomass accumulation (Robinson et al., 2002; Rott et al., 2006). For example, Robinson et al., (2002) showed using nutrient diffusion experiments that algal growth in glacial streams can be phosphorus limited and that artificial phosphorus inputs increase biofilm biomass. Our results similarly suggest that as disturbance intensity declines, nutrient limitation becomes an increasingly important factor determining algal production.

Increased light exposure could have further contributed to low algal biomass in control and low turbidity treatments. For most epilithic communities in freshwater streams, greater light availability promotes algal biomass through increased opportunities for photosynthesis (Vannote et al., 1980). However, increased light exposure can overwhelm the photosynthetic capabilities of algal communities adapted to dark environments resulting in photoinhibition (Holzinger and Lütz, 2006). Photoinhibition is a common phenomenon in clear alpine streams and can limit algal biomass relative to communities growing in turbid meltwaters (Boix Canadell et al., 2021; Martyniuk et al., 2014; Wellnitz and Ward, 2000). Although the communities in this experiment were exposed to 1/20th of light intensities typically incurred in alpine environments, extended periods of constant light exposure (i.e., 16 hours a day) could have also negatively affected algal growth.

Intermediate and high turbidity treatments created a moderate disturbance regime and supplied adequate nutrients which increased algal biomass relative to control, low, and extreme treatments. Moderate levels of mobilized glacial sediment should weaken the disturbance regimes that we hypothesized limited biomass in our extreme turbidity treatment (Biggs et al., 1998; Francouer and Biggs, 2006). For example, intermediate environmental harshness can drive increased epilithic biomass in glacial streams as epilithic communities in glacial streams are often composed of species tolerant to harsh conditions such as scouring and abrasion ((Niedrist et al., 2018; Rinke et al., 2001; Rott et al., 2006). Increased phosphorus concentrations in the intermediate and high turbidity treatments should also provide biofilms with adequate nutrient supply required to support algal growth (Elser et al., 2020; Robinson et al., 2002). The benefits of increased phosphorus supply are especially apparent when disturbance intensity declines in glacial streams as seasonal TP peaks are often associated with greater algal biomass (Robinson et al., 2002; Uehlinger et al., 2010). Together, disturbance and nutrient availability determine in-part by glacial flour inputs are critical factors affecting algal growth in glacial streams.

Turbidity impacts on community composition

Turbidity also impacted epilithic community composition. Taxonomic responses were mainly driven by increased chlorophyte abundances in the intermediate and high turbidity treatments. For example, we observed an increased abundance of *Klebsoridium spp.* (personal observation), a mucous-producing filamentous chlorophyte in communities exposed to intermediate and high treatments (Rindi et al., 2011). Mucous-producing filamentous species may be favoured under moderate turbidity conditions as extracellular polymeric substances (EPS) can trap suspended sediment which bolsters attachment strength and resistance to further disturbance (Mori et al., 2018). Indeed, species adapted to turbid alpine streams often have mucilaginous envelopes associated with increased adherence to substrate (Rott et al., 2006; Wellnitz and Rader, 2003). This process was apparent in our experiment as macroscopic biofilms growing on tiles exposed to intermediate and high turbidity incurred heavy sedimentation throughout the experiment which potentially improved disturbance resistance. Interestingly, chromophyte abundance, which include diatoms and chrysophytes, increased progressively during the experiment in the intermediate and high turbidity treatments. Epilithic communities in algal streams are often composed of chromophytes due to many species having strong attachment strengths (Fell et al., 2018; Niedrist et al., 2018; Rott et al., 2006). In the extreme turbidity treatment, algal abundances were low across groups. Extreme scouring limits biofilm composition to species with compact growth forms and streamlined cell sizes (Biggs et al., 1998; Francoeur and Biggs, 2006). However, streambed disturbances due to extreme turbidity were likely too intense to facilitate colonization, regardless of cell size or growth form type. Lastly, in the control and low biofilm treatments, all algal groups had very low abundances, suggesting that the strength of nutrient scarcity limited the growth of all algal groups equally.

Future Directions

Although this experiment successfully demonstrated how a meltwater turbidity gradient can alter epilithic algal biomass taken from glacial streams, our experimental design could be improved in several ways. First, PAR and UVR are critical spectral components of alpine landscapes that shape epilithic communities (Elser et al., 2020; Rose et al., 2014). However, because of our indoor mesocosm design, experimental biofilms were not exposed to intense PAR and UVR exposure that in-situ biofilms typically incur. Intense light exposure can damage algal cells and photosystems, further inhibiting epilithic biomass accumulation in alpine freshwaters (Martyniuk et al., 2014; Rott et al., 2006; Uehlinger et al., 2010; Vinebrooke and Leavitt, 1999). Incorporating PAR and UVR into our experimental design would likely further suppress biomass, particularly in our control and low turbidity treatments in which little light scattering occurred. We also relied on biomass to quantify the functional impact of glacial flour on epilithic growth. Additionally combining biomass with other growth characteristics that directly measure the functional contributions algae provide to glacial stream ecosystems, such as gross primary production, would provide increased accuracy needed to capture the potential consequences that decreased glacial stream turbidity has on food production for higher trophic levels (Boix Canadell et al. 2021). Lastly, our mesocosm design reduced the environmental harshness inherent to glacial stream environments. Glacial streams are typically near 0°C (Brown et al., 2003), while meltwaters in this experiment were consistently above 10°C. Likewise, mesocosm channels had slow stream velocities compared to rapid flows commonly observed in glacial streams. As temperature and water flow are critical habitat templates that contribute to the structure of epilithic communities in glacial streams, warmer, slower flows may have further contributed to increased biomass observed in the intermediate and high treatments (Sudlow et al., 2023; Uehlinger et al., 2018).

Conclusion:

Decreased meltwater turbidity decreases nutrient supply to epilithic algal communities and reduces the intensity of historically harsh disturbance regimes (Boix Canadell et al., 2021; Uehlinger et al., 2010). Though warmer temperatures, slower streams, and increased water clarity are predicted to increase algal growth in glacial streams as glaciers continue to disappear, we hypothesize that decreased turbidity could instead constrain epilithic biomass as nutrients supplied by glacial sediments become increasingly scarce (Elser et al., 2020; Uehlinger et al., 2010). As algae are a critical food source for higher trophic levels in glacial streams often lacking allochthonous energy subsidies, decreased primary producer biomass could have consequences for the productive capacity of these ecosystems (Bellmore et al., 2022; Niedrist and Füreder, 2018; Zah et al., 2001;). Increased interest in glacial streams as refugia for species currently experiencing habitat loss downstream due to climate change and anthropogenic pressures further emphasizes the significance of glacier loss inhibiting robust trophic energy transfer (Pitman et al., 2021). Further research is now needed to characterize the conditions that promote and constrain primary production in glacial streams as ice loss continues to accelerate into the 21st century.

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Chapter 4: Conclusion

Synthesis

Glacial stream ecosystems are entering a period of rapid change (Milner et al., 2017). The retreat of mountain glaciers globally is causing meltwater streams to become warmer, clearer, with lower flows, and decreased phosphorus inputs (Elser et al., 2020; Hugonett et al., 2021; Milner et al., 2017; Slemmons et al., 2013; Sudlow et al., 2023). These abiotic transitions impact the organisms living with glacial streams, as communities of microbes, epilithic algae, and benthic macroinvertebrates undergo species turnover and, in some cases, the loss of highly specialized biodiversity (Fell et al., 2018; Jacobsen et al., 2012; Wilhelm et al., 2013). Although biodiversity has been a primary research focus as glaciers melt, less is known about the environmental mechanisms driving species responses. Likewise, how glacier loss alters the ecological functions benthic communities provide to glacier stream ecosystems, such as food production and nutrient cycling, is not well studied.

My research provides novel insights into how epilithic algal communities respond to changing environmental conditions in glacial streams experiencing catchment glacier loss. In chapter 2, I show that algal community biomass peaked at intermediate glacial influence and that meltwater turbidity was a strong predictor of algal growth. I hypothesize that turbidity facilitates glacial stream disturbance regimes while also mediating light and nutrient availability. Chapter 3 describes how I tested this hypothesis by subjecting algal communities to glacial meltwater mixed with varying levels of turbidity using a mesocosm experiment in a controlled environment. This experiment supports the results of chapter 2 as algal biomass peaked under intermediate and high turbidity treatments relative to control, low, and extreme treatments.

Short Comings

Pigment-based analyses provide valuable insights into the abundance of algal groups (Wright et al., 2005). Chlorophyll *a*, for instance, is widely used as an acceptable proxy for algal biomass (Baulch et al., 2009). However, algal abundances derived from pigments are strengthened when paired with taxonomic cell counts. Cell counts can inform community biodiversity metrics not available using pigment abundances, such as species richness and turnover (Fell et al., 2018). Unfortunately, the communities sampled in this thesis had low cell abundances and small cell sizes making counts difficult and highly variable at x400 magnification using a light microscope. More refined taxonomic approaches, such as clearing organic matter with H_2O_2 could improve the accuracy of taxonomic data, though at the cost of non-diatom algal groups (Fell et al., 2018).

The relatively short glacial influence gradient used in Chapter 2 could also have limited the statistical power of my multivariate analyses. Specific conductivity was the only statistically significant predictor of pigment-inferred community abundance. A longer gradient composed of an increased number of catchments should capture a greater range of environmental conditions to assist with the identification of predictors for algal community composition. Catchments with greater glacial coverage would particularly benefit this analysis as the maximum glacial coverage sampled in my study was 36%. Though the literature and site reconnaissance in August 2021 indicated that catchments with > 50% coverage contained limited algal growth, incorporating heavily glaciated catchments into this analysis could improve its statistical power (Fell et al., 2018).

The experimental design implemented in Chapter 3 could be improved in several ways. I measured algal biomass using chlorophyll *a* as a proxy for algal growth. However, direct measurements of productivity, such as gross primary production, would more accurately quantify how turbidity affects algal growth (Boix Canadell et al., 2021). Future iterations of this experiment should also collect biofilm C:N, C:P, and C:Chl *a* ratios. These nutritional content ratios could inform how glacial flour affects the food resources algae provide to higher trophic levels in glacial streams (Martyniuk et al., 2014). Lastly, the light source used in my experiment did not accurately replicate the ambient light conditions incurred across high alpine landscapes in the Canadian Rocky Mountains (Serbue et al., in development). The light source within the experimental chamber had approximately 1/20th of the intensity of natural light (Rose et al., 2014; Personal observation). Replicating alpine light environments would improve the hypotheses generated from this experiment.

Future Research

My studies could be expanded upon in many ways. First, while space-for-time study designs are an informative approach for characterizing abiotic and biotic patterns along large temporal scales, long-term data sets provide opportunities to study glacial stream ecosystem succession in real time (Hotaling et al., 2017). Three decades of research in Wolf Point Creek in Glacier Bay, Alaska, over the course of its deglaciation have produced a suite of conceptual models critical to understanding the ecological consequences of glacier loss (Brown and Milner et al., 2012; Milner et al., 2008). Despite their benefits, such long-term studies are rare due to a variety of logistic constraints (Hotaling et al., 2017). In chapter 2, I sampled streams within five easily accessed glaciated catchments across the Canadian Rockies, each at a different stage of glacier loss. Continued visits would benefit the development of the hypotheses put forward in this thesis, particularly as intra- and inter-annual data sets of algal communities are rare.

A future field experiment would complement my survey and lab experiment studies. In-situ experiments are rarely completed for alpine stream ecosystems because of the challenges alpine environments pose. However, field experiments also provide the realism needed to directly test and develop conceptual models for glacier loss impacts on alpine stream ecosystems. For example, Cauvy-Fraunié et al., (2016) experimentally diverted water from an Andean glacial stream to study the consequences of lower flows on benthic communities. For the hypotheses developed in my thesis, field experiments designed to manipulate stream turbidity would further clarify how turbidity impacts epilithic algae. A potential experimental design could be to divert turbid flows into nearby clear streams, or vice-versa, and measure the subsequent algal responses.

Glacier loss is creating new stream channels along previously glaciated terrain (Shugar et al., 2017; Pitman et al., 2021). However, how benthic ecosystems develop in these young streams is largely unknown. For pacific salmon along the west coast of North America, novel water courses fed by melting glaciers could provide suitable habitat refugia for populations currently downstream experiencing habitat degradation (Pitman et al., 2021). How food resources develop in newly formed glacial streams will be critical for determining potential fish colonization (Bellmore et al., 2022). To is quantify the successional patterns of algal communities in newly formed glacial streams, a future study could survey algae along a range of stream ages or succession stages, from young to well established channels.

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