BIOGEOCHEMICAL DYNAMICS AND RESPONSE TO PERMAFROST DEGRADATION IN MCMURDO DRY VALLEY STREAMS, ANTARCTICA

By

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Abstract

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Streams are biogeochemical connectors that transport and transform nutrients and carbon throughout their watershed. This ability can be altered temporarily or permanently by anthropogenic disturbances like climate warming. The ephemeral streams of the McMurdo Dry Valleys, Antarctica [MDV], are 'model systems', with relatively simple ecology and hydrology: they are fed only by glacial meltwater, and perennial microbial communities drive stream ecosystem function. As Antarctic climate warming continues, it is important to understand both current stream biogeochemical processes and how these may alter under a warmer climate regime.

My research goals are to quantify two key MDV stream biogeochemical processes: carbon fluxes and nutrient (N, P) uptake; and to assess how these ecosystems respond to a warming-related thermokarst disturbance. First, I quantified concentration-discharge relationships for dissolved organic carbon [DOC], and found that, despite low organic carbon stocks and large diel changes in discharge, these streams exhibit DOC chemostasis. To explain this behavior, I developed a new conceptual model for DOC generation and storage. Next, I used pulse additions to determine nutrient uptake dynamics for NO₃-N, NH₄-N and PO₄-P in six streams across the Taylor Valley, at nutrient concentrations from ambient to saturation. These streams demonstrated efficient uptake even at concentrations 2-3 orders of magnitude above typical background levels, indicating biotic ability to adjust to large and rapid changes in nutrient levels. Finally, I quantified stream biotic response to a 2012 thermokarst event, which loaded sediment and nutrients into an MDV stream, by using high-resolution satellite imagery to map stream microbial mat activity from 2010 to 2019. Surprisingly, biotic activity *increased* the year after the thermokarst event, indicating that MDV mat communities are resilient to this type of disturbance. We hypothesize that significantly-higher post-thermokarst N and P loads may have aided this rapid recovery.

As a whole, my research advances understanding of essential stream biogeochemistry in this polar desert environment, including how these systems may respond to a warmer future. Findings from these model systems can also advance our understanding of more complex systems, e.g. temperate and tropical streams, where the microbially-driven processes I elucidate are often hidden by other, larger fluxes.

Dedication

To all the friends, family, colleagues, and critters who have helped me through this process: boundless thanks for all of the support, snacks, coffee, constructive suggestions, hiking, dancing, and love – and deep gratitude for reminding me that there is a world beyond my workstation that I should visit from time to time.

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There are many: this could be its own 100-page tome. And, briefly:

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Chapter I

Introduction

Streams are biogeochemical connectors that transport and transform nutrients and carbon through – and throughout – their watershed (Halbedel et al., 2013; Newbold et al., 1982; Webster et al., 2003; Zarnetske et al., 2018). Their ability to do this is shaped by both physical and biological variables (Newbold et al., 1981), and can be altered temporarily or permanently by climate warming and other anthropogenic disturbance (Evans & Davies, 1998; Godsey et al., 2009; Mulholland et al., 2008; O'Brien et al., 2007). My dissertation research focuses on streams in a particular ecosystem: the McMurdo Dry Valleys [MDV], a polar desert on the coast of McMurdo Sound, East Antarctica (77°00'S 162°52'E). This site is part of the NSF-funded Long Term Ecological Research [LTER] network (lternet.edu): the McMurdo [MCM] LTER. As these chapters will demonstrate, stream hydroecosystems in this extreme environment are interesting subjects and worthy of study in their own right; are an important component in the spectrum of research sites documented by the LTER network; and, due to their relatively simple ecology and hydrology (which I describe herein), are a model ecosystem as defined by Vitousek (2004): one where the very simplicity of the system makes it possible to clearly illustrate broadly-applicable ecological concepts.

Research in the MDV takes on additional import and urgency in the context of global warming and warming-related changes, which are accelerating, especially in polar regions (Bromwich et al., 2013; Chapman & Walsh, 2007; Hinzman et al., 2005; McClintock et al., 2008; Post et al., 2009; Steig et al., 2009). While East Antarctica has experienced climate-related changes (IMBIE Team, 2018; Steig et al., 2009), there has not been a warming trend in the MDV (Obryk et al., 2020). However, this region has experienced multiple disturbances that may be

precursors of increased warming and enhanced ecosystem connectivity, including heat waves, floods, rising lake levels, and thaw of both permafrost and lake ice (Gooseff et al., 2017a). In these circumstances, it is essential to both document the existing ecosystem dynamics and learn as much as we can about these ecosystems' resilience and expected responses to warming-related disturbance. To this end, I have studied both fundamental components of MDV stream carbon and nutrient cycling, as well as the ecosystem response over time (10 years total) to a 2012 permafrost degradation and streambank subsidence event.

As noted previously, the MDV are characterized by relatively simple hydrological and ecological systems. These streams are ephemeral, flowing 4-9 weeks/ year during the austral summer, and are fed only by glacial melt (Wlostowski et al., 2016). Mean annual precipitation, which falls as snow, ranges from 3-50 mm annually (Doran et al., 2002; Fountain et al., 2010). Watershed inputs from lateral flow and terrestrial organic matter are negligible (McKnight et al., 1999). These streams flow through large expanses of barren, unconsolidated glacial alluvium (Cozzetto et al., 2013); there are no vascular plants or macrofauna (McKnight et al., 1999). Microbes, in benthic mats and hyporheic biofilm, drive MDV stream ecosystem function, including nutrient and carbon cycling. As a stream ecosystem ecologist, my research focuses on nutrient and carbon fluxes and pools rather than the stream microbial communities; but these communities are the warp and weft that support MDV stream ecosystem functions and, by extension, my dissertation work.

Stream microbial mats are the dominant source of organic carbon in the MDV system, although hyporheic biofilms also contribute (Barrett et al., 2007; Hawes & Howard-Williams, 1998; Maurice et al., 2002). These mats are composed primarily of cyanobacteria, which provide a substantial matrix for diatoms and other microorganisms (Alger et al., 1997; Hawes &

Howard-Williams, 1998; Stanish et al., 2011). They are commonly placed into one of three categories that describe their dominant community: black (primarily *Nostoc* sp.), green (primarily *Prasiola* sp.), and orange (primarily *Phormidium* sp.). The mat phototrophs fix carbon and add it to the system, heterotrophs absorb carbon, and both phototrophs and heterotrophs are subject to decomposition and the accompanying release of dissolved organic carbon (DOC; Spencer et al., 2012). These mats also help move carbon through the ecosystem, in a passive way; mat particles are scoured during the daily high flows and subducted into the hyporheic zone or flushed downstream, towards terminal lakes (Cullis et al. 2014; Heindel et al., 2021). In winter, strong winds carry particles of freeze-dried mats across the landscape, where they collect in streambeds and also on glaciers (Fountain et al., 1999; Moorhead et al., 1999). Some of the latter, glacial particles seed cryoconite holes, and from there can be flushed back into streams (Bagshaw et al., 2013; Porazinska et al., 2004). While we know these mats contribute to instream DOC in multiple ways, we have not known whether or how the instream DOC concentrations they generate change with streamflow.

Both mats and hyporheic microbes are central to stream nutrient cycling. *Nostoc spp.*, which dominate the black mats, are nitrogen fixers that colonize the wetted margins of streams (Alger, 1997; Kohler et al., 2015b). These black mats are also the main source of particulate organic matter that transports N downstream and into the hyporheic zone (Cullis et al., 2014; Heindel et al., 2021). Another important source of N in this system is marine aerosols. They are blown upvalley by strong seasonal winds and tend to accumulate away from the coast, causing the NO₃-N gradient observed in the Taylor Valley (Welch et al., 2010). Both benthic mats and hyporheic biofilm play demonstrated roles in NO₃ uptake and transformation, with measured nitrification in benthic mats and denitrification in the hyporheic zone (Gooseff et al., 2004b;

Kohler et al., 2018; McKnight et al., 2004; Singley et al., 2021). PO₄, on the other hand, is a weathering solute found in stream sediments and valley soils. Its concentrations are highest closer to the coast and decrease as you move inland, towards the Taylor Glacier (Welch et al., 2010). This P gradient is attributed to differences in the parent material rather than the age of the tills, as the soils in this extremely cold and arid climate have weathered slowly and thus are in a very early stage of the Walker & Syers (1976) model of pedogenesis (Bate et al., 2008; Heindel et al., 2017). Like other weathering solutes, PO₄ accumulates in the hyporhic zone and is flushed out at higher flows (Gooseff et al., 2002; Wlostowski et al., 2018). Stream microbes, like all living things, need both N and P for growth and development and drive biological uptake in stream channels. While there have been isolated uptake experiments, we have not studied whole-stream uptake dynamics across the MDV landscape.

As the Antarctic climate continues to warm, MDV ecosystems are likely to experience stronger and more frequent changes, including increased warming and increased liquid water in the system; as a result, will see increasing landscape and ecosystem connectivity as well as increasing potential for disturbances such as floods and thermokarst events (Gooseff et al., 2017a; Fountain et al., 2014). This heightens the importance of understanding how warmingrelated changes will impact both the physical and biological systems. A study of MDV stream ecosystem disturbance inherently involves studying how the microbial colonies respond. There have been a handful of studies that examine microbial mat responses to scour and to changing flow conditions. We know these mats do recover from scour, but slowly, taking multiple seasons to rebuild lost biomass (Kohler et al., 2015a). They are sensitive to substrate and tend to colonize desert pavement and not sandy, shifting soils (McKnight et al., 1998; Alger et al., 1997). All three categories of microbial mats are sensitive to flow conditions, but each type responds differently to high versus. low flow versus changing flow (Kohler et al., 2015b). We also know they are resilient to desiccation, even long-term (10-year) desiccation (McKnight et al., 2007). There have also been physical disturbance studies in MDV streams; these have focused on relatively recent thermokarst developments in the Garwood and Taylor Valleys (Gooseff et al., 2016; Levy et al., 2013; Sudman et al., 2017). Thermokarst formations are a type of subsidence feature; they are parallel to karst formations in limestone geographies (i.e. sinkholes in Florida), but instead of groundwater dissolution of limestone, they are caused by thawing permafrost. Both of these thermokarst areas have been well-characterized physically, but the biological impacts have not been examined.

My three research chapters aim to fill these knowledge gaps. Chapter 2 focuses on organic carbon transport and storage. MDV streams have very low DOC concentrations compared to temperate streams, in the range of 0.1 to 2 mg C l⁻¹ (Aiken et al., 1996). This is not surprising, given the low the abundance of organic carbon in the surrounding landscape (Barrett et al., 2007; McKnight et al., 1998). Chemical analysis clearly shows that this organic carbon is autochthonous, derived from microbial biomass (Aiken et al., 1992; Aiken et al., 1996; Foreman et al., 2013; Smith et al. 2017). MDV stream discharge is characterized by large diel and interannual changes, controlled by energy balance on the glacier surface, and can increase up to an order of magnitude in a single day (Conovitz et al., 1998). In this chapter, I leverage mathematical models and 30 years of MCM LTER water chemistry and discharge data to determine the concentration-discharge relationship for DOC in MDV streams. From my results, I develop a new conceptual model for DOC storage and generation in these streams.

Chapter 3 quantifies nutrient uptake dynamics for NO₃, NH₄, and PO₄ in six streams across the MDV's Taylor Valley. Similar to organic carbon, ambient nutrient concentrations in

MDV streams tend to be low compared to most temperate streams (for my study streams and years, median DIN = 0.04 mg/L and median SRP = 0.006 mg/L; supported by e.g. Barrett et al., 2007; Welch et al., 2010). Both N and P concentrations differ across the valley, causing a landscape gradient of increasing N:P with distance from the coast (Welch et al., 2010). To quantify uptake metrics (i.e., uptake length (S_w [L]) and uptake velocity (V_f , [L/T])) for each nutrient species, I conducted a series of pulse nutrient additions in each stream. I also assessed potential drivers of nutrient uptake. This study represents the first time NH4 uptake dynamics have been quantified in the MDV and is also the first nutrient uptake experiment conducted at this geographic scale, i.e. across the Taylor Valley vs. in a single stream. The results enable comparisons of NO₃, NH4, and PO₄ uptake dynamics across the Taylor Valley and around the world.

Chapter 4 focuses on stream ecosystem response to a thermokarst disturbance. Thermokarst is best known from Arctic research studies; it develops when permafrost thaws, causing land subsidence (Hinzman et al., 2005; Kokelj et al., 2013). If themokarst develops near a stream, it can increase the instream nutrient and sediment loads by several orders of magnitude and have profound physical and biological effects on stream biogeochemistry and ecosystem function (Bowden et al., 2008; Kokelj et al. 2013). In January 2012, researchers discovered thermokarst development on one fork of Crescent Stream, Crescent West (Gooseff et al., 2016). Physical changes due to this disturbance have been well documented (Gooseff et al., 2016; Sudman et al., 2017), but assessing biotic impacts and recovery has been difficult. Two obstructions to this assessment are the lack of pre-thermokarst data and the lack of large-scale or whole-stream biomass data. To resolve these issues, I use remote sensing imagery and analysis to assess annual biotic change in Crescent West between January 2010 and January 2019. I also

quantify whole-stream biotic percent cover and areal cover (m²) for four stream reaches in the

MDV. This is one of the first studies to assess how MDV streams will respond to a warming-

related disturbance, as well as one of the first to use these remote sensing techniques to

determine MDV biotic activity. It also provides the first estimates of whole-stream biotic cover

for these streams.

As a whole, the work in this dissertation provides new information on biogeochemical

cycling and its drivers in MDV streams, as well as insight into how these systems will respond to

warming-related thermokarst disturbance.

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Chapter II

Dissolved Organic Carbon Chemostasis in Antarctic Polar Desert Streams

Abstract

Dissolved organic carbon (DOC) is a key variable impacting stream biogeochemical processes. The relationship between DOC concentration (C) and stream discharge (q) can elucidate spatial and temporal DOC source dynamics in watersheds. In the ephemeral glacial meltwater streams of the McMurdo Dry Valleys (MDV), Antarctica, the C-q relationship has been applied to dissolved inorganic nitrogen and weathering solutes including silica, which all exhibit chemostatic C-q behavior; but DOC-q dynamics have not been studied. DOC concentrations here are low compared to temperate streams, in the range of 0.1 to 2 mg C l⁻¹, and their chemical signal clearly indicates derivation from microbial biomass (benthic mats and hyporheic biofilm). To investigate whether the DOC generation rate from these autochthonous organic matter pools was sufficient to maintain chemostasis for DOC, despite these streams' large diel and interannual fluctuations in discharge, we fit the long-term DOC-q data to a power law and an advectionreaction model. Model outputs and coefficients of variation (CV) characterize the DOC-q relationship as chemostatic for several MDV streams. We propose a conceptual model in which hyporheic carbon storage, hyporheic exchange rates, and net DOC generation rates are key interacting components that enable chemostatic DOC-*q* behavior in MDV streams. This model clarifies the role of autochthonous carbon stores in maintaining DOC chemostasis and may be useful for examining these relationships in temperate systems, which typically have larger sources of bioavailable autochthonous organic carbon than MDV streams but where this autochthonous signal could be masked by a stronger allochthonous contribution.

Plain Language Summary

This study assesses the relationship between instream dissolved organic carbon (DOC) concentrations and streamflow in the McMurdo Dry Valleys, Antarctica (MDV). DOC comes from the breakdown of organic matter (e.g., plants, microbes). In temperate streams, DOC mostly comes from plants and soil outside of the stream; this is not the case in the MDV, where most DOC comes from inside the stream. There are no vascular plants, but some MDV streams host abundant microbial mats - like a shag carpet on the streambed. Organic material from these mats is stored in the underlying streambed sediments, which are saturated with streamwater. MDV streamflow is derived entirely from glacial melt in summer and varies on a daily and interannual basis. We used two different models to evaluate whether and how DOC changed with changing streamflow. Both models indicated that stream DOC concentrations are relatively stable (0.1-2 mg 1⁻¹) over large changes in streamflow (1-1000 1 s⁻¹). We conclude that the streambed storage zone is key to maintaining DOC concentrations across all streamflow conditions. We present a conceptual model that may also provide insight into the role that streambeds play in contributing DOC to streams in non-polar environments.

1 Introduction

Dissolved organic carbon (DOC) is a key variable in stream ecosystems, influencing stream biogeochemistry (Halbedel et al., 2013; Zarnetske et al., 2018), supporting aquatic food webs (Tank et al. 2010), and forming a major constituent of global carbon fluxes (Battin et al., 2009; Meybeck, 1982). In glaciated systems, DOC fluxes can be a major source of organic carbon (OC) to the ocean or terminal lakes (Hood et al., 2020; McKnight et al., 1999). Understanding how instream DOC concentration (C) changes with discharge (*q*) can elucidate

where and how DOC is generated in the watershed, the relative controls of surface and subsurface (hyporheic) processes (Castro & Hornberger, 1991; Singley et al., 2021), how DOC source dynamics respond to changing watershed conditions (i.e. snowmelt, flooding, irrigation, etc.; Evans & Davies, 1998; Godsey et al., 2009; Thompson et al., 2011), and whether OC is limited by supply or hydrologic transport (Creed et al., 2015; Thompson et al., 2011; Zarnetske et al., 2018). Possible C-q relationships include chemostasis (little variation in C with changes in q), source limitation (decreasing C with increasing q), and transport limitation (increasing C with increasing q; Godsey et al., 2009; Zarnetske et al., 2018), each of which are indicative of different spatiotemporal DOC source dynamics throughout a watershed.

In temperate and boreal streams, allochthonous DOC from upstream and upland sources typically dominates the instream DOC fluxes, especially in lower-order streams (Burns et al., 2016; Hale & Godsey, 2019, Vannote et al., 1980). The riparian zone is a particularly large contributor in these watersheds (84% of allochthonous fluxes; Dick et al., 2015). These allochthonous DOC inputs can either support chemostasis as they are mobilized by higher flows, buffering the increase in discharge (Hale & Godsey, 2019; Jantze et al., 2013; Mulholland & Hill, 1997) or can lead to greater variability or 'flashiness' of DOC-*q* responses in small or low-flow streams (Creed et al., 2015; Rue et al., 2017). The tendency towards DOC chemostasis generally increases as stream order increases because each allochthonous input contributes a smaller portion of the total load (Creed et al., 2015).

In polar deserts and other glaciated, low-OC environments, small changes in DOC fluxes can have disproportionately large effects; therefore, DOC-*q* dynamics in these systems may be particularly sensitive to source dynamics. Recent studies have compared DOC-*q* relationships in glaciated and non-glaciated watersheds in Alaska and the European Alps (Boix Canadell et al.,

2019; Fellman et al., 2014; Hood et al., 2020). In both Alpine and Alaskan proglacial streams, DOC concentrations were low (< 0.1-2 mg C l⁻¹) but increased with vegetation coverage (Boix Canadell et al., 2019; Fellman et al., 2014). In Alaska, meltwater streams in less-vegetated watersheds were source limited for DOC. As watershed vegetation cover increased, these DOC-*q* dynamics shifted to transport limitation (Hood et al., 2020). Fluorescence and δ^{13} C-DOC signatures also shifted from having a proportionately high amount of δ^{13} C-enriched, microbiallyderived carbon in the less-vegetated watersheds to having predominantly vascular plant-derived, humic DOC as vegetation increased (Fellman et al., 2014). In Alpine streams with typically low vegetation cover, the DOC-*q* dynamics were close to chemostatic; similar to the Alaskan studies, these dynamics shifted to transport limitation as vegetation cover increased (Boix Canadell et al., 2019).

In the McMurdo Dry Valleys (MDV), the instream DOC-q relationships and source dynamics of DOC at the watershed scale have not previously been studied. Previous MDV research has examined stream C-q relationships for silica and other weathering solutes (Wlostowski et al., 2018) and dissolved inorganic nitrogen (DIN; Singley et al., 2021); each of these relationships was chemostatic. For weathering solutes, the chemostatic behavior reflects their low equilibrium concentrations (C_{eq}) and the rapid weathering rates that are characteristic of MDV streams (Gooseff et al., 2002; Lyons et al., 1997; Wlostowski et al., 2018). For DIN, chemostasis reflects both the low ambient dissolved N concentrations and the increasing release of hyporheic N stores with increasing discharge (Kohler et al., 2018; Singley et al., 2021).

C-q relationships in the MDV are shaped by the region's distinctive biology and hydrology. During the austral summer, intermittent glacial meltwater streams flow for 4-10 weeks and most are first or second order, flowing into a terminal lake. The only water source is

glacial melt: precipitation and hillslope inputs are negligible, and there is no deep groundwater interaction (Gooseff et al., 2004; McKnight et al., 2004). Thus, stream discharge is characterized by strong diel pulses, generated by the sun's movement around the horizon, with increases in streamflow up to an order of magnitude in a single day (Conovitz et al., 1998). During cold or cloudy periods, when there is no meltwater source, streamflow is supplied by hyporheic drainage (Conovitz et al., 1998). Interannual streamflow varies widely based on seasonal differences in cloud cover and glacial albedo, which impact the rate of melt (Gooseff et al., 2017; Obryk et al., 2018).

MDV streams flow through unconsolidated, highly porous glacial alluvium (Cozzetto et al., 2013), which is strikingly uniform throughout the Valleys (Fountain et al., 1999). These streams are well-connected to their hyporheic zones (Gooseff et al., 2004), which are key sites for weathering and microbial activity (Kohler et al., 2018; Lyons et al., 1997). Isotopic analysis shows that the hyporheic zone is an important source of autochthonous, remineralized N to MDV stream channels, via the processing and retention of N from sloughed black microbial mats (i.e. from POM released by black, *Nostoc*-dominant mats, usually at high flows; Kohler et al., 2018). Hyporheic zone extent is determined by the thaw depth, which increases throughout the summer flow season (Gooseff et al., 2002; McKnight et al., 2004; Runkel et al., 1998). Typically, the seasonal maximum thaw depth is < 1 m (Conovitz et al., 2006).

The MDV landscape is poor in organic carbon. Unlike the proglacial streams in Alaska and the Alps, MDV streams have no vascular plants; the sparse riparian vegetation is comprised of mosses (McKnight et al., 1999). The primary DOC source in these streams is autochthonous, from benthic microbial mats (Barrett et al., 2007; Hawes & Howard-Williams, 1998; McKnight et al., 1998). These mats represent sources of both dissolved and particulate organic matter in the stream ecosystem (Aiken et al., 1996; Cullis et al., 2014). Living phototrophs may release some of their fixed carbon to streams, and both phototrophs and heterotrophs are subject to decomposition and DOC release (Spencer et al., 2012). At daily high flow conditions, mat material from the black, *Nostoc*-dominated mats in the stream margins is scoured, flushed downstream, and may be trapped within the substrate matrix by hyporheic downwelling (Heindel et al., 2021), eventually providing DOC to both the hyporheic zone waters and the stream water. The presence of chlorophyll pigment, biogenic silica, and preserved diatom frustules supports a microbial mat source of this hyporheic-zone POM (Heindel et al., 2021). The mat-derived DOM in the streamwater may also degrade to DOC during transport (Cullis et al., 2014).

Hyporheic biofilm is another potential DOC source (Maurice et al., 2002); this biofilm has not been quantified in the MDV, but it is known to play a central role in the transformation and processing of instream C and N (Heindel et al., 2021; Koch et al., 2010; Singley et al. 2021). The instream DOC concentrations in MDV streams are generally low compared to temperate streams, and in line with other glacial meltwater streams, with a median value below 1 mg C l⁻¹ (Aiken et al., 1996). The microbial biomass source of the DOC is reflected in the low humic content and spectroscopic properties (less than 10% humic fraction; Aiken et al., 1996; Aiken et al., 1992).

Other potential DOC sources include glacial runoff (Foreman et al., 2013; Smith et al., 2017) and aeolian deposition (Fountain et al, 1999; Moorhead et al., 1999). While glacial runoff from supraglacial streams and cryoconite holes supplies some DOC to the stream systems, the source concentrations are quite low; cryoconite hole concentrations range from 0.41-0.79 mg C l⁻¹ (Bagshaw et al., 2013) and supraglacial stream DOC concentrations range from 0.44-1.68 mg C l⁻¹, with a fluorescence signature that is consistent with a microbial source (Foreman et al., 2013;

Smith et al. 2017). While these supraglacial sources would supply measurable DOC to streams, DOC concentrations could not be maintained from glacier to stream sampling point (0.7-7.5 km downstream, see Table 1) without additional DOC inputs, due to DOC sinks. Documented instream DOC sinks include biotic uptake by heterotrophic organisms in mats and in the hyporheic zone (Koch et al., 2010; Kohler et al., 2018) and potential sorption on mineral surfaces in the hyporheic zone (McKnight et al., 2002). Distal to the glacier, the supraglacial sources are likely a minimal source of DOC compared to the thick, perennial microbial mats that are present in the channel and wetted margins of streams (Alger et al., 1997).

Local aeolian deposition is also a source of particulate organic matter (POM) to MDV streams (Fountain et al., 1999; Moorhead et al., 1999). Strong seasonal winds redistribute sandsized particles of soil and dessicated microbial mats (found in dry streambeds, ponds, and moat areas) across the landscape (Deuerling et al., 2014; Diaz et al., 2018, Moorhead et al., 1999). Most of this redistribution occurs during the winter months, when streambeds and ephemeral ponds are seasonally dry and sporadic föhn winds reach upwards of 37 m s⁻¹ (Deuerling et al., 2014, Fountain et al. 1999). There are also summer wind events that occur during the flow season (Deuerling et al., 2014), but these would be less likely to slough and redistribute the microbial mats that are now wetted or submerged. Therefore, aeolian contributions to stream POM would be unlikely to increase during the flow season and would have the strongest signal in the earliest flushing flows of each season as meltwater first contacts and carries the wintertime aeolian deposits. The primary goal of this research is to determine how the existing autochthonous matter pools in MDV streams shape the DOC-*q* relationships. Potential relationships include source-limitation (as seen in the Alaskan streams of Hood et al., 2009,

2020), transport limitation, and chemostasis. A second research goal is to identify key factors controlling the DOC-q relationship in these streams.

To quantitatively characterize the DOC-q relationship in MDV streams, we chose three common C-q metrics. One metric assesses the relative variance in concentration and discharge data (Musolff et al., 2017; Thompson et al., 2011), the second was generated by a power-law model (Doyle et al., 2005; Godsey et al., 2009; Zarnetske et al., 2018), and the third by an advection-reaction model (Maher, 2011; Maher & Chamberlain, 2014; Wlostowski et al., 2018). To assess potential controls on the DOC-q relationship, we ran multiple regression analyses, exploring: the influence of instream biomass (ash-free dry mass [AFDM]) and stream length on DOC concentrations; the influence of the three DOC-q shape parameters on the net generation time scale (a supply parameter that describes the timescale of net DOC generation and transport from source to stream water); and the influence of these shape parameters on fluid transit time (a transport parameter; Wlostowski et al., 2018). To assess differences in biological vs. physical controls, we compare DOC-q dynamics to those Wlostowski et al. (2018) found for silica (Si)-q. We consider Si to be a representative weathering solute based on Si isotopic composition research by Hirst et al. (2020): they determined that the dissolved silica in streamwater is both in equilibrium with and largely attributable to the formation of secondary Si minerals in the hyporheic zone; while diatoms are present in the stream and hyporheos, they do not contribute significantly to the composition of dissolved Si. Due to the low levels of organic carbon and the highly variable discharge in these streams, we hypothesize that we will find a source-limited, diluting DOC-q relationship.

2 Study Site

For this study, we selected seven streams in the Lake Fryxell basin of the MDV (Figure 1). These streams all have a long-term (30-year) record of discharge and water chemistry, and four of them have established long-term transects for sampling microbial mats. Details regarding the datasets and data collection follow, under 'Methods: Data sets'. The streams were selected to represent a wide range of microbial mat coverage, from Lost Seal Stream with no visible mats to Green Creek with thick and widespread mats. Aiken Creek's microbial mat coverage exists primarily in Many Glaciers Pond, a large pond that hosts abundant microbial mats and is situated between the source glacier and the stream gage/water sampling site.

These streams also vary in length (measured from source to stream gage/ water sampling location). With weathering solutes such as Si, stream length is a common proxy for hyporheic influence; longer streams contain higher concentrations of these solutes due to a greater extent of hyporheic zone weathering (Gooseff et al., 2002; Lyons et al., 1997). This variation in stream length allows us to test for the impact of stream length on DOC concentrations and DOC-q dynamics.

3 Methods

3.1 Data sets:

The McMurdo Dry Valleys Long Term Ecological Research program (MCM LTER) has maintained a network of 17 stream gages and water chemistry sampling sites throughout the MDV since 1993. Here we analyze DOC-q relationships and compare them to Si-q relationships in seven Lake Fryxell basin streams (Figure 1) using the long-term q, solute concentration, and microbial mat biomass data sets from 1990-2019. These and other long-term data sets are hosted at mcmlter.org and at the Environmental Data Initiative (environmentaldatainitiative.org).



Figure 1: Map of Fryxell Basin with study streams highlighted and stream gage locations indicated by black-and-white bullseye icons (left); and a photograph of Crescent Stream depicting a typical stream path from glacier source to terminal lake (right). Inset map shows the location of the Dry Valleys in Antarctica.

All seven study streams are gaged and have in-situ sensors that yield continuous records of temperature, stage, and specific electrical conductance at 15-minute intervals during the 4-10 week summer flow season. Seasonally-adjusted rating curves are used to convert stage to volumetric discharge (Q, L sec⁻¹). Volumetric discharge was then converted to Darcy velocity (q, m day⁻¹) using the following equation:

$$q = \frac{Q}{A_x} = \frac{Q}{\left[(w_c + 2w_{hz})z_{thaw}\right]} \tag{1}$$

where A_x = the cross-sectional stream area (m²), w_c = the stream channel width (m), w_{hz} = the width of the hyporheic zone (m), and z_{thaw} = the thawed active layer depth (m; Wlostowski et al., 2018). We assume that $w_c = 4$ m, $w_{hz} = 5$ m, and $z_{thaw} = 1$ m based on prior observations of channel and hyporheic extent (Northcott et al., 2009) and maximum annual thaw depth below streams

(Conovitz et al., 2006). We chose our parameter values both to be consistent with the weathering solute analysis by Wlostowski et al. (2018), which facilitates comparison between the geogenic and biogenic processes, and because they are reasonable for this system. The hyporheic zone 'fills' before streamflow is observed, and therefore its width would be relatively consistent throughout the flow season. The active layer depth does increase during the flow season (Conovitz et al. 2006); however, the timescales for discharge and active layer change are very different. Discharge varies widely on a diel basis throughout the season, while active layer depth increases incrementally throughout the season. While individual calculations may be altered slightly by our assumption, the trends across 29 seasons of data would be more robust. We chose to use Darcy velocity for these analyses because it explicitly incorporates hyporheic flowpaths and flow velocities, which are important both to calculate total fluid transit time and as sites of organic and inorganic carbon storage and transformation (Mulholland et al., 1997; Welch et al., 2010). It is also consistent with modeling of weathering solute *C-q* relationships in MDV streams by Wlostowski et al. (2018), which facilitates comparison.

Water chemistry samples are collected approximately weekly during the flow season for most streams. Due to intermittent streamflow and other logistics, sampling does not occur at the same time each week. Water chemistry samples are analyzed for many solutes, including weathering ions and DOC, following the methods reported in Koch et al. (2010; for DOC and nutrients) and Welch et al. (2010; for anions and cations). All samples are filtered within 24 hours of collection and kept chilled (4°C) until analysis. Nitrile gloves are worn during sample collection to minimize organic contamination of the samples. DOC samples are collected in precombusted amber glass bottles and filtered through a combusted glass microfiber filter (WhatmanTM GF/CTM 47 mm filter) into a second precombusted amber glass bottle.

Immediately after filtering, samples are acidified to a pH of 2 to 3 with a 50% solution of hydrochloric acid to drive off inorganic carbon, stored dark and chilled (4°C) until transport to Crary Lab, then analyzed for DOC using a non-purgeable organic carbon method. The exact instruments have changed over the 30-year sampling record, but they have always been Shimadzu instruments that utilize a 680°C combustion catalytic oxidation method and NDIR detector, with a carrier gas of ultra zero grade air; and the samples (filtered and acidified) have always been sparged before being injected into the combustion tube (Koch et al. 2010). The current instrument, in use since 2015, is a Shimadzu TOC-L CPN with a method detection limit of 0.1 mg C 1⁻¹ (K.A. Welch, personal communication, 03 May 2022), which is the same limit reported for previous instruments (Koch et al. 2010). It is dedicated to running low-OC stream and glacier samples to keep the catalyst clean and the detection limit low (K.A. Welch, personal communication, 03 May 2022). Silica samples are filtered through 0.4-µm Nucleopore polycarbonate membrane filters into HDPE bottles prerinsed with deionized water. Dissolved Si is measured colorimetrically following the methods of Mullin and Riley (1955). This paper uses "Si" in reference to the colorimetrically detected dissolved silicon species, H₄SiO₄.

Microbial mat samples have been collected along established transects in various MDV streams since 1994, and their ash-free dry mass (AFDM) is used to estimate long-term biomass variation within and across the sample streams. Four of our study streams have consistently-sampled, long term microbial mat transects: Canada, Delta, Green, and Von Guerard. Our analysis of mat material focuses on these four streams.

The abundance and distribution of MDV microbial mats are dependent upon mat type, streambed substrate, and discharge (Kohler et al., 2015; McKnight et al., 1998). The mats are commonly divided into three categories for biomass assessments, based on dominant color and community composition: orange, green and black (Alger et al., 1997; McKnight et al., 1998). Each type of mat has a different habitat preference, with black, *Nostoc*-dominated mats preferring the wetted margins of streams and orange (*Phormidium* sp. dominated) and green (*Prasiola* sp. dominated) mats preferring the channel (Alger et al., 1997; Kohler et al., 2015; Niyogi et al., 1997; Vincent et al., 1993).

Mat sampling occurs in January and has been annual since 2002; prior to 2002, these samples were collected approximately every three years. Each sampling visit collects 2-4 plugs of each type of microbial mat near each transect, using a 1.7 cm diameter brass cork borer. These samples are analyzed for AFDM by drying at 100°C for 24 hours, weighing, ashing at 450°C for 4 hours, then re-weighing to determine the mass lost to combustion (Kohler et al., 2015). Water chemistry samples are collected as part of the microbial mat sampling protocol, and analyzed using the same protocols as the other water quality samples, as described above.

3.2 Data analysis:

3.2.1: Determining the DOC-q relationship:

To answer our first question, whether the DOC-q relationship is chemostatic, transportlimited or source-limited, we used three established methods to quantitatively assess the shape of the C-q relationship. First, we fit the DOC and q data to a power-law model:

$$C = aq^b \tag{2}$$

where *C* is the concentration (mg l⁻¹), *q* is the Darcy velocity (m day⁻¹), and *a* and *b* are empirically fitted parameters (Doyle et al. 2005, Zarnetske et al. 2018). The best-fitting *b* value
for each stream represents the log-log slope of the DOC-*q* relationship and indicates whether it is transport-limited (b > 0.20), source-limited (b < -0.20) or chemostatic ($-0.20 \le b \le 0.20$; Godsey et al., 2009).

Second, we fit the data to an advection-reaction model to determine the Damköhler number (Da), which describes whether the C-q relationship is transport- or source-limited. This work is based on a model developed by Maher (2011) and Maher & Chamberlain (2014), which was previously applied to weathering solutes in MDV streams by Wlostowski et al. (2018):

$$C = C_{eq} \frac{\frac{\gamma D w}{q}}{1 + \frac{\gamma D w}{q}}$$
(3)

where *C* is the concentration (mg l⁻¹), C_{eq} is the solute equilibrium concentration (mg l⁻¹), γ is a dimensionless constant (= e²), *Dw* is the Damköhler coefficient (m day⁻¹), and *q* is the Darcy velocity (m day⁻¹). Note that *q* is used in the original model and in applications to the MDV streams to account for flow occurring outside of the stream channel (i.e., hyporheic exchange). Equation 3 is fit to the *C*-*q* observations by optimizing *C*_{eq} and *Dw*. The model assumes an exponential distribution of fluid transit times along an idealized flow path. It provides a process-based interpretation of the *C*-*q* relationship, where model outputs are tied to physically-meaningful parameters.

We used the model output Damköhler coefficient (Dw) to calculate the dimensionless Damköhler number (Da) per Equation 4. Da is also equal to the ratio of τ_f (fluid transit time) to τ_{gen} (the net DOC generation timescale; parallel to τ_{eq} , the equilibrium timescale, for weathering solutes):

$$Da = \frac{Dw}{q} = \frac{\tau_f}{\tau_{gen}} = \frac{\tau_f}{\tau_{eq}} \tag{4}$$

For our analyses, we used Da_{med} , the Damköhler number calculated using the median q for that stream.

Fluid transit time (τ_f) represents the average time that water spends in surface and subsurface flow paths, and is approximated as the ratio of channel length to seepage velocity $(\frac{q}{\phi})$:

$$\tau_f = \frac{L\phi}{q} \tag{5}$$

where *L* is the length of the stream (m) and ϕ is the porosity of hyporheic sediments (m³ m⁻³). Stream length (*L*) is measured from the source to the stream gage location, where water samples are collected. Hyporheic porosity is assumed to be uniform and = 0.4 for our study streams, which all flow through sandy alluvial soils. These simple approximations are appropriate given the simplicity of the MDV stream hydrologic system, which can be compared to a natural flume (Gooseff et al., 2004; Wlostowski et al., 2018).

The net DOC generation time scale (τ_{gen}) represents the characteristic time for DOC to be generated and transported from the source to the streamwater. When used to simulate the transport and reaction of weathering solutes, τ_{gen} is replaced with τ_{eq} , a reaction term that incorporates the influence of kinetics of mineral weathering, temperature, sediment composition, and erosion rate (Maher, 2010; Wlostowski et al., 2018). The generation timescale τ_{gen} is calculated by rearranging and simplifying Equations 4 and 5, to yield:

$$\tau_{gen} = \frac{\tau_f}{Da} = \frac{L\phi}{qDa} = \frac{L\phi}{Dw} \tag{6}$$

Per Equation 4, Da < 1 indicates that $\tau_{gen} > \tau_f$ and that the solute flux is source-limited. Da > 1indicates that $\tau_{gen} < \tau_f$ and that the solute flux is transport-limited (Maher & Chamberlain, 2014; Wlostowski et al., 2018).

Third, we calculated the ratio of the coefficients of variation for the long-term records of *C* and *q* (*CV_c/CV_q*) for each stream (Musolff et al., 2017; Thompson et al., 2011). Chemostasis is defined as a stable concentration across a range of discharge, which would correspond with a $CV_c/CV_q \ll 1$. Chemodynamic (flushing or diluting) relationships would have a $CV_c/CV_q > 1$ (Thompson et al., 2011).

3.2.2: Determining DOC-q controls:

We expect that both microbial mat biomass and τ_f will be strong indicators of the DOC-q relationship. We also expect that MDV streams with higher mat biomass will have both higher DOC concentrations and less-diluting DOC-q relationships, and that τ_f , not τ_{gen} , will control between-stream variation in the DOC-q relationship, because DOC generation rates per area of biomass (DOC source material) would not vary much across streams while longer fluid transit times would allow more contact with this DOC source material in the stream and hyporheos.

To test the influence of mat biomass, we quantified annual microbial mat biomass (ashfree dry mass, AFDM) based on the long-term MCM LTER data record. We focused this analysis on the four modeled streams with a consistent long-term algal sampling record: Canada, Delta, Green, and Von Guerard. If a stream had multiple mat sampling transects, we chose the one closest to the stream gage, which is where the DOC samples are collected. We used regression analyses to assess whether the average annual DOC concentration was a function of microbial mat biomass for each stream. We tested both the average and the highest biomass values for each season, since the high-biomass mats are likely to generate more DOC. We also tested for significant relationships by stream, by mat type and by within-stream location (i.e. margins vs. channel, or black vs. orange + green mats). We also tested for significant relationships between DOC concentration and stream length. Our hypothesis that biomass controls the DOC-q relationship is supported if DOC concentrations have a positive relationship with stream biomass or stream length.

To test the influence of τ_f and τ_{gen} on between-stream differences in the DOC-qrelationship, we compared each of these timescale parameters to the three DOC-q shape parameters (Da, b, and CV_c/CV_q) that indicate the degree of dilution or chemostasis for each stream. Significant correlations (positive or negative) between either τ_f or τ_{gen} and these shape parameters would indicate that timescale parameter controls between-stream differences in DOC-q. If the three shape parameters become more chemostatic as τ_f increases, this would support our hypothesis that τ_f controls between-stream variation in DOC-q dynamics.

We ran the same series of analyses on Si, to provide a comparison to a true weathering solute. This updates the Wlostowski et al. (2018) analysis with more recent data.

4 Results

MDV DOC-*q* relationships are strongly chemostatic, showing little variation in DOC concentration over four orders of magnitude of *q* (Figure 2). While CV_c/CV_q values for DOC are higher than for Si in all of our study streams (Table 1, Table S1, Figure 2), the range of these ratios is greater than the analytical uncertainty and is consistent across decades of high-quality

DOC data. DOC concentration is also consistent across the study streams regardless of stream length (Figure 3a) or mat biomass (Figure S1). Regressions between DOC as a function of biomass and DOC as a function of stream length showed no significant relationships (p > 0.05for all comparisons), which is not surprising as there are no apparent spatial (Figure 3a) or temporal (Figure 4) trends in DOC concentration. Of the seven study streams, only Aiken Creek shows a significant difference in mean DOC concentrations, with a higher mean DOC concentration than any other stream (Aiken Creek's mean = $1.17 \text{ mg C } 1^{-1}$, means of other streams range from 0.41-0.82 mg C l⁻¹, p < 0.05 for all comparisons). This difference is likely driven by Many Glaciers Pond, which supports relatively high microbial mat biomass (Sakaeva et al., 2016). Water residence time in the pond increases the overall fluid transit time for Aiken Creek, equating to increased water contact with a DOC source. In contrast, the weathering solutes (e.g., Si), while chemostatic, do have concentrations that increase with stream length (Figure 3b), due to the greater amount of substrate supplying weathering solutes in longer streams (Gooseff et al., 2002). Unlike DOC concentrations, the residence time in Many Glaciers Pond does not impact Si concentrations in Aiken Creek: weathering solute concentrations have a physical upper limit (chemical equilibrium). Also, the pond's thick microbial mats are full of diatoms (Sakaeva et al., 2016); while diatoms have a negligible impact on instream Si concentrations, they would become a Si sink in the pond due to the longer residence time.



Figure 2: Visual inspection shows the chemostatic relationships of DOC and Si solute concentrations as a function of discharge (q) in seven MDV streams; Si concentrations are scaled for better visualization. Si represents a weathering solute signal and DOC represents a biological solute signal. The dotted line indicates where a pure dilution relationship would fall on the graph. The script used for these visualizations is based on code developed by Wlostowski et al. (2018), to facilitate comparisons between our findings.



Figure 3: These boxplots indicate DOC and Si concentrations ordered by stream length, from source to gage box, in the 7 study streams. The stream is indicated by the boxplot color, and stream length is on the x-axis.



Figure 4: These scatterplots visualize the distribution of DOC-q relationships by water year in each stream. The y axis shows DOC concentration in mg C l^{-1} , the x axis shows discharge (q, m day⁻¹) and each water year is represented by a different color. Individual water years are difficult to identify but broader timesteps (e.g. 2-5 years) are linked by similar shades, giving a general impression of differences over time. There are no significant trends in these data.

All three shape parameters quantitatively characterize MDV DOC-q relationships as chemostatic rather than diluting or flushing behavior (Table 1). Using b, the slope of the best-fit power-law relationship, all streams except Aiken meet Godsey et al.'s (2009) definition for chemostasis: b values range from -0.22 to -0.02, with a mean value of -0.08. Aiken Creek (b = -

0.22) is likely an outlier because of Many Glaciers Pond, which contains a high amount of organic matter; the pond would impact both DOC concentration and DOC variability due to changing flow dynamics. The CV_c/CV_q analysis shows that all streams have CV_c/CV_q values less than 1, indicating chemostasis (Thompson et al., 2011): values range from 0.36 to 0.83, with a mean value of 0.63 (Table 1). For comparison, Wlostowski et al. (2018) found that CV_c/CV_q values for four Fryxell Basin weathering solutes ranged from 0.07 to 0.76 with a mean value of 0.26, and Thompson et al. (2011) found that typical CV_c/CV_q values for both weathering and biologically-derived solutes in temperate streams ranged from 0.15 to 3.5 with a mean of 0.68. Using a Da_{med} (Da calculated at median q for each stream) derived from the best-fit advection-reaction model, MDV streams have a $Da_{med} > 1$, indicating they are transport-limited (Maher, 2011; Maher & Chamberlain, 2014; Wlostowski et al., 2018). Da_{med} values range from 1.70 to 131.23, with a median value of 43.15. Streams with smaller magnitude b values (i.e. values closer to 0) also have higher Da_{med} values, showing agreement between the power law and advection-reaction models.

Stream	Length	$q_{ m med}$	$ au_f$ med	C_{eq}	b	CVc/CVq	Damed
	(m)	$(m day^{-1})$	(day)	(mg l ⁻¹)			
Aiken	2760	48.14	22.93	1.40	-0.22	0.83	1.70
Canada	700	54.93	5.10	0.38	-0.03	0.36	11.55
Crescent	5500	34.56	63.66	0.52	-0.02	0.36	100.56
Delta	7510	24.07	124.81	0.42	-0.02	0.78	49.66
Green	700	69.74	4.02	0.46	-0.11	0.74	3.36
Lost Seal	2000	75.29	10.63	0.43	-0.03	0.83	131.23
VG	4700	22.83	82.33	0.57	-0.14	0.51	4.00

Table 1. DOC Model Parameters and Shape Factors, by Study Stream

The regression analyses between the shape parameters and both τ_f and τ_{gen} show no significant relationships and most have low R² values (all p > 0.05, most R² < 0.10, Figure 5). There are two near-linear relationships for DOC: between Da_{med} and τ_{gen} (Figure 5b, p = 0.0638, R² = 0.53) and between b and τ_{gen} (Figure 5f, p = 0.0501, R² = 0.57): Da_{med} and b both increase (b approaches 0) as τ_{gen} decreases, i.e. as the DOC generation time decreases. If these trends were significant, they would indicate that DOC generation dynamics, not transit time, determine the degree of DOC-q transport-limitation in MDV streams.

As expected, Si-*q* relationships are quantitatively chemostatic across all streams (Table S1). Values for *b* range from -0.13 to -0.01, with a mean of -0.06; CV_c/CV_q values are all less than 1 and range from 0.09-0.27, with a mean of 0.17; and Da_{med} values are all greater than 1 (1.62-41.11, median of 25.93), indicating transport limitation. For Si regressions, all shape parameters had a significant relationship with τ_f (all p < 0.05, R² 0.73-0.89; Figure S2). Both *b* and CV_c/CV_q approach zero as τ_f increases, and Da_{med} is positively correlated with τ_f ; this indicates that Si-*q* chemostasis increases with fluid transit time and that τ_f determines the degree of Si-*q* transport-limitation in MDV streams. These results support the findings of Wlostowski et al. (2018).

5 Discussion

5.1 DOC-chemostasis in MDV streams

Analysis shows that DOC-*q* relationships are strongly chemostatic in MDV streams (Figure 2), with DOC concentrations showing little variation across orders of magnitude of discharge. There is also little net variation across streams (Figure 3) or years (Figure 4); apart from Aiken Creek, there is no significant difference in the mean DOC concentrations of the study streams. Therefore, it is not surprising that there was no relationship between DOC

concentration and either stream length or mat biomass, both of which are more variable, relatively, than mean DOC concentrations.

DOC $CV_{c'}/CV_q$ values are higher than Si $CV_{c'}/CV_q$ for all streams (Table 1, Table S1, Figure 2). This finding is consistent with differences in the source materials of the two solutes. Silicate materials that make up the soils and streambeds of the MDVs are relatively uniform throughout the Fryxell basin (Gooseff et al., 2002), while DOC sources are inherently patchy. Benthic biomass in streams is largely dictated by substrate and hydrologic regime (Kohler et al., 2015). The perennial mats thrive on rocky, stable desert pavement and are sparse or nonexistent on sandy, mobile reaches, which do not accommodate much establishment and growth (McKnight et al., 1998). Thus hyporheic POM, as a source for hyporheic and ultimately stream DOM, is also expected to be spatially dispersed (Heindel et al., 2021).

For all streams, the slope of the DOC-q power-law relationship (b) is close to zero, there is little variation in C over a wide variation in q, and the steady-state advection-reaction model shows these streams to be predominantly transport-limited (Table 1). Together, these findings support a chemostatic DOC-q relationship across all of the study streams. There is betweenstream variation in the degree of DOC chemostasis (Table 1), but no significant correlations to indicate whether this variation is controlled by transport or generation.

Our hypothesis, that MDV DOC-q would have source-limited dynamics similar to those found in Alaskan proglacial watersheds (Hood et al., 2020), was not correct. On the surface, our finding of DOC chemostasis is similar to that of Boix Canadell et al. (2019), but the two systems likely exhibit similar dynamics for different reasons. The MDV has no vascular plants and essentially 0% watershed vegetation cover, while the streams Boix Canadell et al. (2019) observed had relatively high percent vegetation cover, even in the highly-glaciated watersheds

(25-57% vegetation cover in glaciated sites, 51-100% in non-glaciated sites). The higher % vegetation cover in the Alpine streams provides a true riparian zone, supplying a DOC source at higher flows and thus supporting chemostasis (Creed et al., 2015; Dick et al., 2015; Seibert et al., 2009). In contrast, the MDV does not have watershed vegetation to act as a DOC source.

5.2 DOC generation - biological control

That DOC-*q* relationships are chemostatic across all streams is surprising, given the small amount of organic carbon in this landscape. Further, DOC generation is somehow supplied across several orders of magnitude of *q* from autochthonous organic carbon alone. The breakdown of POM primarily occurs in the stream channel and hyporheic zone; it is largely a biological process driven by the physical sloughing (particulate organic matter release) of in-channel mats and by decomposer microorganisms in the mats and hyporheic sediments (Cullis et al., 2014; Heindel et al., 2021). While there are differences between biogenic (DOC) and geogenic (Si) solutes, we expected that some aspect of the numerical model would help to explain DOC chemostasis, similar to the findings of Wlostowski et al. (2018) when they applied the same reactive transport model to chemostatic weathering solutes in these streams.

Chemical equilibrium is not a factor for DOC in the same way it is for weathering solute chemostasis, and MDV DOC concentrations do not increase with stream length (Figure 3). Instead, the DOC "equilibrium" concentration (C_{eq}) represents DOC source and sink processes upstream of that sampling point and the balance of DOC generation and exchange specific to that sampling location. Thus the DOC net generation timescale (τ_{gen}) represents the average time required to reach this balance point of sources, sinks, storage and exchange. It could be interpreted as the ratio of the "equilibrium" concentration to the net DOC generation rate (NGR), or

$$\tau_{gen} = \frac{C_{eq}}{NGR} \tag{7}$$

Because C_{eq} is relatively steady across these streams (Table 1), variations in the NGR control differences in τ_{gen} . Streams that have the slowest NGR would have the highest τ_{gen} , while streams that have more rapid NGR would have a lower τ_{gen} . This interpretation is supported by the fact that streams with the lowest τ_{gen} are more strongly chemostatic (Figure 5).

This model assumes that, across the reach, generation and uptake occur on similar timescales as each other and as the sub-diel changes in discharge. While we do not have direct measurements for DOC generation rates, we know this can occur at the same timescale as the roughly diel flood pulses. Koch et al. (2010) measured DOC and other solutes at multiple points along their study reach during a 31-hour NO3⁻ addition in Huey Creek, another stream in the Fryxell Basin of the MDV; hydrologically, this study spanned two flood pulses and two troughs. The study focused on hyporheic uptake and generation, as the reach (and Huey Creek in general) did not have visible benthic mats. Koch et al. (2010) found evidence of sub-reach scale hyporheic DOC production or release during and shortly after the flood pulses, which maintained DOC chemostasis at the downstream sampling point. They also calculated DOC net areal uptake during the low-flow periods, when discharge was relatively stable, and found it ranged from 0.1 to 0.4 mg m⁻² hr⁻¹ (Koch et al. 2010). These findings support our model's assumption: hyporheic DOC is generated quickly enough to be flushed into the stream with the diel flood pulses, thus supporting chemostasis.



Figure 5: These scatterplots depict the values of the three DOC-q shape parameters (y-axes) and either the mean transit time at median q (τ_f ; x-axes for plots a, c, e) or the generation time scale (τ_{gen}); x-axes for plots b, d, f). There are no significant relationships in any of these regressions (all p > 0.05). In contrast, Si relationships for the shape parameters and τ_f are all significant (see Wlostowski et al., 2018, and this paper's supplemental materials).

5.3 Controls on DOC-chemostasis

We initially expected that the amount of source material, or algal mat biomass, would be one key factor influencing DOC-chemostasis. However, we find no apparent relationship between DOC concentration and algal mat biomass (Figure S1). This finding may be due to the microbial mat sampling protocols; these samples are point measurements along a transect and do not represent areal biomass coverage of the stream. A dataset that measured whole-stream mat biomass may have generated different results.

With the exception of Aiken Creek, there is little variation in mean DOC concentration across most our study streams (Figure 3), which agrees with the findings of Aiken et al. (1996). Aiken Creek has both a significantly higher mean DOC concentration and a wider range of concentrations compared to other study streams. This can likely be attributed to the influence of mat-rich Many Glaciers Pond on the Aiken stream channel. The higher DOC mean can be explained by the high mat density and longer water residence time in the pond. The wider DOC range can be explained by the natural variation in stream discharge. When the system experiences relatively high diel flood pulses, water would move through the pond quickly and spill into lower Aiken Creek without much time for solute generation; this is shown in Figures 2 and 4, where DOC shows a decreasing trend when q exceeds ≈ 20 m day⁻¹.

We hypothesized that fluid transit time (τ_f) would be an important control on the DOC-qshape and would explain between-stream differences in degree of chemostasis, because a longer transit time (in longer streams, and/or in lower flow streams) would allow more opportunity for DOC generation. This hypothesis is not supported by the shape parameter analysis (Figure 5). Like Wlostowski et al. (2018), we found that τ_f controlled between-stream differences in the shape of the C-q curve for Si; however, it appears that neither τ_f nor τ_{eq} provide this control for DOC.

We propose that the relationships between τ_f , τ_{gen} , and other transport metrics (Figure 5) also indicate the hyporheic influence on DOC chemostasis. While τ_f is not correlated with

transport limitation, it clearly contributes to transport dynamics (Equation 4). Fluid transit time varies with flow path length, and hyporheic flow paths are both longer and have a lower velocity than in-stream flow paths. In the MDV, where sediment porosity is relatively uniform across streams (Fountain et al., 1999), total hyporheic area and potential flow path length increases with stream length. At median discharge, longer streams have longer mean fluid transit times due to these longer hyporheic flow paths (p = 0.0004, $R^2 = 0.92$).

Controls on DOC chemostasis in the MDV must differ from temperate stream controls. In temperate streams, the chemostatic DOC-q balance is maintained by an allochthonous DOCsource that is accessed at higher flows (Hale & Godsey, 2019; Mulholland & Hill, 1997); this may also have occurred in DOC-chemostatic glaciated Alpine streams (Boix Canadell et al., 2019). There are no large allochthonous carbon sources in the MDV. In spite of this, the MDV DOC-q balance is remarkably consistent across time (decades), range of discharge (multiple orders of magnitude), and channel length (Figures 2, 3, 4). We propose that in the MDV, intermittently-connected areas in the hyporheic zone and wetted margins may serve as carbon storage sites, analogous to riparian and hillslope carbon storage in temperate streams. This scenario would explain the difference between our findings and those of Hood et al. (2020), whose Alaskan proglacial watersheds may not have had the organic stores from microbial mats to buffer their DOC sources against glacially-mediated variations in discharge. To help explain this mechanism, we propose the following conceptual model, consisting of four processes (or 'bins'): generation (source), loss (sink), storage, and hyporheic-surface water exchange. These bins are described in detail, below.

5.4 Conceptual model for dissolved carbon chemostasis:

First we will describe the four 'bins' or processes that our model contains: generation, loss, storage and exchange; then we will visualize and detail the model itself. The primary DOC source to MDV streams is benthic microbial mats that grow on the bed and wetted margins of streams (Barrett et al., 2007; Hawes & Howard-Williams, 1998; McKnight et al., 1998). Secondary sources are POM from these mats, which may be buried or lodged in stream interstices, and hyporheic microbial biofilm. Unlike in temperate streams, there are negligible allochthonous DOC sources. DOC sinks include biotic uptake by heterotrophic organisms in mats and in the hyporheic zone, and chemical sorption.

Because of the large diel and seasonal variations in streamflow, the stream channel expands and contracts on a daily and seasonal scale. The hyporheic zone also expands over the course of the flow season due to active layer thaw, and it may contract during low or no-flow periods. These changes impact both hyporheic storage and the exchange of water and solutes with the stream channel. High flows access and flush stored hyporheic solutes into the stream, while lower flows "strand" (isolate) damp sediments, allowing them to accumulate solutes (Figure 6). At lower flows, hyporheic organic matter is temporarily isolated, either by diminished exchange or reduced preferential flow paths (Figure 6a); but it continues to produce DOC, creating a pool that can be mobilized to maintain chemostasis at higher flows (Figure 6b, c). The expansion and contraction of streamflow also impacts the benthic DOC source, as the margin and some in-channel mats are alternately wetted and dried, i.e., connected and disconnected from releasing DOC into the channel. The wetted margins of streams may also act as a DOC storage site at lower flows, as subsurface POM and surface mats continue to release DOC into the wetted margins but have little to no DOC exchange with the stream channel. In effect, the isolated sites

in both the margins and hyporheic zone are parallel to riparian storage zones in temperate streams; they function as storage pools of organic carbon, buffering DOC chemostasis when they are tapped at higher flows.

The long-term datasets used in these analyses do not distinguish between in-channel and hyporheic DOC sources. However, a hyporheic DOC source is plausible based on other research: we know that the hyporheic zone contains POM that is sloughed from microbial mats (Cullis et al., 2014; Heindel et al., 2021; Singley et al., 2021), and that this organic matter contributes dissolved nitrogen and likely other solutes to the stream channel (Singley et al., 2021). We also know that the hyporheic zone of MDV streams is an active site of DOC uptake and generation that occurs on sub-diel timescales (Koch et al, 2010).



a. low flow

Figure 6: Stream cross-section illustrating the conceptual model for hyporheic DOC generation and storage at low (a), median (b) and high flows (c). Orange, black, and striped boxes

represent microbial mats. Blue represents the stream water and the blue/ brown areas represent the saturated sediments of the near and deep hyporheic zone (HZ, above). The arrows represent exchange between stream and hyporheic waters. At each flow level, the hyporheic zone acts as a generation, storage and release site for DOC, buffering the DOC-q relationship against the large changes in q this system experiences. This parallels the role of the riparian zone in temperate stream DOC chemostasis. At very high flows, mats also slough POM (represented by the small, floating orange and black boxes), some of which is buried in the hyporheic zone to seed future DOC generation.

At median flow, with a moderate water volume, many but not all of the mats would be flooded and releasing DOC into the stream channel (Figure 6b). Hyporheic extent and exchange would be moderate, and some areas would be well-connected with the channel, mobilizing DOC, while others would not. The wetted areas that were not well-connected with the channel would continue to break down organic matter into DOC, creating some storage pockets that would only be accessed at relatively high flows.

At low flows, with a low water volume, the decrease in *q* would be compensated for by the decrease in DOC release (Figure 6a). Fewer mats would be submerged, decreasing the amount of DOC released to the stream water. Hyporheic exchange would be lower, and the hyporheic zone itself might contract during an extended period of very low or no flow. DOC generation would continue in the wetted mats and hyporheic zone (where there is POM). Less of the DOC generated and stored in the hyporheic zone would be released to the channel.

At high flows, the increase in q would be compensated for by a flushing of the stored DOC that was generated at lower flow levels (Figure 6c). All of the mats would be submerged, increasing the surface area of mat that would release DOC to the stream channel. At higher flows, there is also more likely to be sloughing and entrainment of mat material that would subsequently generate (stored then flushed) DOC.

There are several ways to test this new conceptualization of hyporheic storage and exchange impacting instream DOC. One method would be to use probes or repeated sampling to monitor hyporheic DOC at various flows and distances from the stream, to test whether there actually is a pool of organic carbon waiting to be mobilized at higher flows. More accurate measurements of hyporheic biomass would also be useful, to support and quantify the existence of a hyporheic OM source. These measurements would inform both the conceptual model and improve the accuracy of tested relationships between DOC and biomass. In addition to fieldwork, this conceptual model could be tested by developing a DOC-specific mathematical model to describe the instream flows. It would include terms for the storage and exchange components described here, in addition to terms for the more widely-accepted sources and sinks.

6 Conclusions

In streams, DOC can be generated by the breakdown of detrital POM and through release from periphyton and hyporheic biofilms. In spite of the sparse POM storage in MDV streams, concentrations of DOC are chemostatic across several orders of magnitude in q. In temperate streams, organic matter is largely allochthonous and DOC chemostasis is understood to be influenced by legacy pools of this allochthonous carbon in the riparian zone. As there is no 'riparian zone' nor pools of allochthonous carbon in the MDV, we must seek a different explanation for the chemostatic DOC-q behavior. This explanation must involve the primary MDV DOC source: microbial mat material, either in the channel or buried in the hyporheic zone.

We propose a conceptual model in which DOC chemostasis is a product of the interaction of the four processes (bins): generation, uptake, storage (here, primarily hyporheic), and exchange. The hyporheic storage and exchange locations have not previously been explored for DOC. In the MDV, autochthonous hyporheic POM and wetted-margin microbial mats are the carbon pool supporting DOC chemostasis, paralleling the allochthonous riparian/ hillslope pools in temperate systems.

This is the first examination of the dynamics impacting DOC chemostasis in the MDV. It is likely that the processes influencing DOC chemostasis were not fully captured by the long-term data record we studied. Although this study does not provide a definitive solution to the causes of DOC chemostasis in the MDV, it does provide clues to the processes involved and can inform future investigations and models. It also provides insight into the ways autochthonous carbon contributes to DOC-q relationships in systems where the autochthonous influence is obscured by the dominance of allochthonous carbon inputs.

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Data availability

The stream gage data (Gooseff & McKnight, 2019a-c; Gooseff & McKnight, 2021a-d); water chemistry data (Lyons, 2016; Lyons & Welch, 2016); and microbial mat data (McKnight, 2019) are available at the McMurdo Long Term Ecological Research website and the Environmental Data Initiative.

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Chapter III

N and P uptake dynamics in Antarctic glacial meltwater streams

Abstract

Understanding the dynamics of stream nutrient uptake and transport is integral to creating watershed biogeochemical budgets, managing watersheds, and understanding stream ecosystem health and productivity. Potential controls on uptake include the amount of transient storage in streams, ambient nutrient concentrations, and the standing stock of microbial mat biomass. In the McMurdo Dry Valleys, Antarctica [MDV], the intermittent, glacial meltwater streams are integral connectors of the other major landscape units: glaciers, soils, and lakes. Some aspects of nutrient uptake are known, but most studies have a relatively narrow geographic focus (i.e. one stream). This study uses TASCC-method pulse addition experiments to characterize nutrient uptake dynamics for NO₃, NH₄, and PO₄ in six stream reaches that span the Taylor Valley. We also assess potential controls on uptake length (S_w [L]) and uptake velocity (V_f [L/T]) across these streams. Pulse nutrient addition methods like TASCC are commonly used to calculate uptake dynamics at a range of nutrient concentrations, from ambient to saturation; this enables understanding of current conditions as well as prediction of nutrient dynamics under changing conditions. For NO₃-N, ambient S_w ranged from 1.54-1503 m and ambient V_f ranged from 0.0061-104.68 mm/min; for PO₄-P, ambient S_w ranged from 55-670 m and ambient V_f ranged from 0.038-7.48 mm/min; and for NH₄, ambient S_w ranged from 83-254 m and ambient V_f ranged from 0.02-7.63 mm/min. These values are comparable to those reported in temperate streams. Evidence of rapid nitrification was found in one of the MDV streams, with a pulse of NO₃ observed following the injected pulse of NH₄. We confirm the importance of the hyporheic zone as a key site for NO₃ uptake and processing in MDV streams, and demonstrate that it is also important for PO₄ and NH₄. Our results also indicate that MDV stream biota have the capacity to assimilate and transform nutrients both at and well above current ambient limits, which has implications for ecosystem function under climate warming: MDV stream biota may be able to thrive under the projected increases in nutrient availability, and reduce or prevent increased nutrient loading to the terminal lakes via stream channels.

Introduction

Stream nutrient retention and export dynamics are important for understanding the status of an aquatic ecosystem, watershed biogeochemical budgets, and a stream reach's impact on downstream water bodies (Covino et al., 2010b; Dodds et al., 2002; Mulholland et al., 2008, Newbold et al. 1982, Webster et al., 2003). Quantifying these dynamics can improve watershed management practices (Ensign & Doyle, 2006; Martin et al., 2011; Payn et al., 2005), and facilitate understanding and prediction of watershed and stream ecosystem responses to climate warming, nutrient loading, and other anthropogenic changes (Covino et al., 2021; Dodds et al., 2002; Gibson et al., 2015; O'Brien et al., 2007).

The nutrient spiraling concept is fundamental to understanding stream ecosystems. Briefly, the concept describes the cyclic path of a nutrient atom in streams: downstream hydrologic transport, uptake, and release. Thus it is influenced by both physical and biological factors (Newbold et al., 1981) and depends on the relative strength of biological retention processes versus hydrological transport processes (Wollheim et al., 2006). Nutrient uptake is a key component of biological retention, and is itself a function of multiple processes, including: nutrient background concentrations and ratios (Dodds et al., 2002; Martin et al., 2011; Mulholland et al., 2002; Munn et al., 1990; O'Brien et al., 2007); biotic activity in the stream and

hyporheic zone (Duff & Triska, 1990; Gooseff et al., 2004; Newbold et al., 1983); and the amount of transient storage in a stream (Ensign & Doyle, 2005; Mulholland et al., 1997), which increases contact time between biota and a particular water parcel. This study will examine how these three key processes affect nutrient uptake in streams of the McMurdo Dry Valleys, Antarctica [MDV].

Nutrient uptake is typically quantified using nutrient addition experiments, where a known mass of nutrient and conservative tracer are added to a stream and sampled at a known time and distance downstream (e.g. Dodds et al., 2002). These nutrient additions are designed to either increase overall concentrations (e.g., Bernhardt et al., 2002) or isotopically-labeled concentrations (e.g., Webster et al., 2003) of the target nutrient; and either raise these concentrations to a steady-state (e.g., Dodds et al., 2002; Mulholland et al., 1997), or to multiple measured concentration levels (e.g., Covino et al., 2010b; Payn et al., 2005; Tank et al., 2008). Raising the overall concentration in a steady-state addition can artificially lengthen uptake values (Mulholland et al., 2002); but isotopically-labeled nutrients, which avoid this issue, can be expensive to use and analyze (Payn et al., 2005), as well as difficult to deploy in larger streams (Tank et al., 2008) and in sensitive or protected systems, where permits for isotopic work may be denied. Both multi-level (Payn et al., 2005) and pulse (Covino et al., 2010b; Tank et al., 2008) nutrient addition techniques were developed to resolve these issues.

Commonly-used uptake metrics include uptake length (S_w , [L]) and uptake velocity (V_f , [L/T]; e.g., Newbold et al., 1981). S_w represents the average distance a nutrient travels downstream before it is removed from the water column. V_f combines S_w with estimates of average streamflow (Q, [L³/T]) and stream width (w [L]; $V_f = Q/(S_w*w)$). Because V_f controls

for differences in water depth and velocity, it facilitates comparisons between streams (Bernhardt et al., 2002).

Nutrient concentrations typically influence nutrient uptake dynamics (Dodds et al. 2002; Earl et al. 2006; O'Brien et al., 2007). Other studies have identified three different models to describe the influence of nutrient concentration on stream nutrient uptake kinetics: 1) saturation or Michaelis-Menten (Covino et al. 2010; Dodds et al., 2002; O'Brien et al., 2007); 2) 'decreased efficiency' (Mulholland et al., 2002; Earl et al., 2006; O'Brien et al., 2007); and 3) increasing uptake with concentration, called both 'first order' and 'biostimulation' kinetics in the literature. 'First order' describes a linear increase in uptake with concentration, while 'biostimulation' is broader and can also encompass nonlinear increases (Diemer et al., 2015; Dodds et al., 2002; O'Brien et al., 2007). All three models are depicted in Figure 1. The first two models, saturation and decreased efficiency, are by far the most commonly described in literature.

For the Michaelis-Menten or saturation model, nutrient uptake plateaus once concentrations reach a given level, indicating that the system is saturated and that organisms' nutrient processing rate has reached its limit (Figure 1, green dot-dash line). The 'decreased efficiency' or 'efficiency loss' model posits that systems do not saturate: as concentrations increase, organisms continue to increase uptake; however, uptake rates slow and the uptake process becomes less efficient (Figure 1, dark orange dashed line; e.g., Mulholland et al., 2002). The 'first order' or 'biostimulation' kinetic model describes increasing uptake as nutrient concentrations increase, indicating that the organisms maintain (1st order) or even increase (biostimulation) their uptake efficiency at increasingly high concentrations (Figure 1, solid line; e.g., Diemer et al., 2015; O'Brien et al., 2007). There is no established mechanism to explain this

third model, although there are multiple hypotheses. Covino et al. (2012) found this uptake response occurred in streams with chronically-high nutrient loads. Diemer et al. (2015) found it occurred in streams where the watersheds had a history of wildfire disturbances. Both Diemer et al. (2015) and Rodriguez-Cardona et al. (2016) suggested that biostimulation may be a form of 'priming effect', as described in soil microbial literature (Blagodatskaya & Kuzyakov, 2008), i.e. accelerated microbial activity in response to increased nutrient availability.

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Figure 1: A visual depiction of the three nutrient uptake models (saturation, efficiency loss, and 1^{st} order/biostimulation), and their signature patterns for uptake length (S_w), uptake velocity (V_f), and uptake (or process) rate (from O'Brien et al., 2007).

Stream responses to increased nutrient concentrations can differ between short-term increases in a reach's nutrient concentration, e.g. through nutrient additions or storm pulses, and long-term, ambient differences, e.g., across a landscape gradient (O'Brien et al., 2007). Biological uptake responses to short-term increases tend to exhibit Michaelis-Menten kinetics and saturate at higher nutrient concentrations (Covino et al., 2010a; Payn et al. 2005), especially in streams with lower ambient concentrations (Earl et al., 2006). In contrast, biological uptake under higher long-term or ambient nutrient concentrations tends to become less efficient, but does not exhibit saturation (Dodds et al., 2002; Mulholland et al., 2008), likely because microbes are able to adapt to their environment (O'Brien et al., 2007).

In the MDV's Taylor Valley, nutrient concentrations vary across a geographic gradient of increasing NO₃-N:PO₄-P ratios with increasing distance from the coast, which occurs in soils, streams, glaciers and lakes. This gradient is caused by both an increase in NO₃-N moving inland, due to accumulation of marine aerosol deposition; and a decrease in PO₄-P moving inland due to changes in the soil parent materials (Bate et al., 2008; Heindel et al., 2017)¹. This gradient may also indicate limitation of the lower-concentration nutrient. Vitousek & Farrington (1997) found that ecosystems in lower-P soils were P-limited, while those on higher-P soils were N-limited. In the MDV, we know that microbial mats in two streams in the Fryxell Basin, closer to the coast (Green Creek and Aiken Creek), showed increased biomass and *chl-a* production when exposed to long-term NO₃-N supplementation via nutrient-diffusing substrates (Kohler et al., 2016). This suggests that these high-P, low-N streams are experiencing N-limitation based on the ambient geographic gradient, similar to the findings of Vitousek & Farrington (1997). We hypothesize

¹ Note that here, soil P does not decrease with till age (unlike, e.g., the Hawaiian chronosequences (Vitousek & Farrington, 1997, among others)). While MDV till age ranges from ~ 20,000 to 1,500,000 years, all of the soils are in a relatively early stage of the Walker and Syers (1976) model of pedogenesis due to decelerated weathering in this extremely cold and arid climate (Heindel et al., 2017).

that the existing N and P gradients will drive nutrient limitation, and that there will be a coincident gradient of increased uptake of the limited nutrient: e.g., N uptake velocities will be higher near the coast and P uptake velocities will be higher inland.

Biotic processes of uptake and transformation also influence nutrient retention. It makes intuitive sense that stream reaches with more instream primary producers will have greater biological demand for nutrients; and this intuition is supported by research. Increased benthic biomass, of microbial mats in particular, has been linked to increased nutrient uptake in temperate streams (Bernhardt et al., 2003, 2005; Harvey et al., 2003; Marti et al., 1996).

Transient storage zones impact both physical and biological nutrient retention. Transient storage is one of the key processes controlling the physical transport of stream solutes, along with advection and dispersion (Stream Solute Workshop, 1990; Wagner & Gorelick, 1986). Stream transient storage zones are areas where the downstream flow of water is delayed, relative to advection and dispersion, by either an in-channel feature (e.g. turbulent flow, an eddy, or a deep pool), or by hyporheic flowpaths (e.g., Ensign & Doyle, 2005). These areas of slowed flow are often 'hotspots' for nutrient uptake and transformation (Briggs et al., 2010; Gooseff et al., 2004) and have been linked with increased uptake velocities and amounts (Ensign & Doyle, 2005; Mulholland et al., 1997). One common method to estimate advection, dispersion, and transient storage is to conduct an injection tracer study and analyze the stream solute breakthrough curve. Transient storage strongly influences the delayed portion, or tail, of this curve (Bencala & Walters, 1983; Zarnetske et al., 2007).

Both transient storage and benthic biomass impact MDV stream nutrient uptake and retention. In MDV streams, transient storage is primarily hyporheic (Cozzetto et al., 2013; Gooseff et al., 2003), and can be large compared to the wetted channel area (Runkel et al., 1998).
The porous hyporheic zone (Cozzetto et al., 2013) is dynamic, gradually expanding throughout the flow season as the active layer thaws and contracting again in late summer when the active layer begins to re-freeze (Conovitz et al., 2006). It is an important storage and processing site for organic carbon and nutrients (Heindel et al., 2021; Kohler et al., 2018), thus influencing nutrient uptake dynamics (Koch et al., 2010; Singley et al., 2021). Benthic microbial mats do not occur in all MDV streams or reaches; but where they exist, they increase MDV nutrient uptake (e.g., Gooseff et al., 2004; Kohler et al., 2018) and reduce N and P export to terminal lakes (McKnight et al., 2004). Whole-stream nutrient uptake experiments show that substantial NO₃ uptake occurs in both the channel (mats) and in the hyporheic zone (Gooseff et al., 2004; Koch et al., 2010; McKnight et al., 2004), while PO₄ uptake occurs primarily in the channel (McKnight et al., 2004). Denitrification occurs in hyporheic sediments and microbial mats, on relatively short (sub-diel) timescales (Gooseff et al., 2004; Koch et al., 2010; Maurice et al., 2002). Organic matter sloughed from N-fixing microbial mats (Nostoc sp.) accumulates in the hyporheic zone (Heindel et al., 2021), where it is processed by the resident biota (Kohler et al., 2018). This creates a store of mineralized N that can be stored in the hyporheic zone, especially at lower flows (Singley et al., 2021), and that, when mobilized, is assimilated by downstream benthic mats (Kohler et al., 2018). We expect that the mat biomass-nutrient demand relationship described in temperate streams (e.g. Bernhardt et al., 2003) will be even stronger in the relatively simple streams of the MDV, and that higher microbial mat biomass will correlate with higher nutrient uptake velocities (V_f) and lower nutrient spiraling lengths (S_w). While transient storage varies temporally and perhaps spatially, we expect increasing levels of transient storage to correspond to greater hyporheic uptake, i.e. stronger uptake in the tail of the breakthrough curve(s).

Streams in the MDVs are frequently described as connectors of glaciers, soils and terminal lakes in this landscape (e.g., Gooseff et al., 2017; McKnight et al., 1999). Other studies have conducted uptake experiments for NO₃ and PO₄ in various Fryxell Basin streams (e.g. Green Creek: Gooseff et al., 2004; McKnight et al., 2004; Runkel, 2007; Huey Creek: Koch et al., 2010). However, in spite of their central role in MDV landscape connectivity, stream nutrient uptake dynamics have not been measured across the geographic gradient, which spans multiple lake basins, and have not included the study of NH₄ dynamics. The goals of this study are to quantify NO₃, NH₄, and PO₄ uptake across the Taylor Valley's nutrient gradient; to characterize NH₄ retention in the MDV; and to determine whether nutrient uptake dynamics are governed by background concentration, benthic biomass, or differences in transient storage in these desert streams. To accomplish this, we use nutrient addition experiments to characterize the NO₃, NH₄, and PO₄ retention dynamics of these MDV streams. To assess potential controls on nutrient retention, we conduct this study in streams with varying benthic biomass coverage (Alger et al., 1997) that lie along a geographic gradient of nutrient background concentrations (Welch et al., 2010). We also quantify the transient storage component for each of our nutrient additions and assess its influence on nutrient uptake dynamics.

Study site

The McMurdo Dry Valleys are located at ~77° S latitude, abutting the Ross Sea (Figure 2). This is the largest ice-free region of the continent and has 4 primary landscape units: glaciers, open soils, ice-covered lakes, and stream channels. The polar desert streams of the MDV have relatively simple ecology and hydrology. There are no vascular plants or macrofauna; benthic and hyporheic microbial communities drive stream ecosystem productivity and function (Hawes & Howard-Williams, 1998; McKnight et al., 1999). These intermittent streams are fed primarily by glacial meltwater and flow 4-9 weeks per year during the austral summer (Gooseff et al., 2017; McKnight et al., 2004; Wlostowski et al., 2016). Streamflow is variable on diel and seasonal timesteps and is characterized by strong diel flood pulses generated by solar energy balance on the source glaciers (Conovitz et al., 1998). Stream channels are well-connected to their hyporheic zones (Gooseff et al., 2004) and flow through unconsolidated, highly porous glacial alluvium (Cozzetto et al., 2013), which is strikingly uniform throughout the MDV (Fountain et al., 1999). These hyporheic zones are key sites for microbial activity (Heindel et al., 2021; Kohler et al., 2018; Maurice et al., 2002). MDV streams are oligotrophic, with low ambient loads for carbon and nutrients, including NO₃, NH₄, and PO₄ (Barrett et al., 2007; Welch et al., 2010; Figure 3). Background N:P stoichiometry varies along a spatial gradient, with low N:P at the coast and higher N:P inland (Welch et al., 2010; updated in Figure 4).



Figure 2: Map of the Taylor Valley, MDV with study streams indicated by magenta markers and stream basins indicated by blue boxes. The coast of the Ross Sea is barely visible on the eastern edge of the map. Note that "C", Crescent Stream in Fryxell Basin, represents two study sites: Crescent has two forks, east and west, and nutrient additions were performed on both forks. The inset map shows the location of the MDV within Antarctica.



Figure 3: This boxplot depicts background nutrient concentrations for the study nutrients in each stream, based on almost 30 years of MCM LTER water chemistry data. Streams are arranged in alphabetical order, and the y-axis was scaled to 500 ug/l (removing some high-end outliers in each stream) for improved visualization of the box-and-whisker plots. If arranged in order of distance from the coast, they would read: Von Guerard, Crescent, Green, Priscu, Lawson.



Figure 4: This figure updates the geographic N:P gradient (for NO₃-N and PO₄-P), reported by Welch et al. (2010), with more recent water chemistry data. The increase in N:P moving inland

is due to changes in the absolute concentrations of both N and P, i.e. increases in N and decreases in P with increasing distance from the coast (Welch et al., 2010). NH4-N is found in very low (near detection limit) concentrations across the landscape and would not alter this gradient.

For this study, we selected six different stream reaches along this spatial N:P gradient, from Von Guerard Stream nearest the coast to Lawson Creek farthest inland (Figure 2, Table 1), to test our hypotheses. Not only do our study sites vary by location along the N:P gradient, but also by observed microbial mat coverage and, potentially, transient storage, allowing us to test our hypotheses regarding controls on MDV nutrient uptake.

Distance from Reach Nutrient Mat biomass Stream coast (km) addition (AFDM. length mg/cm^2) (m)date(s)209 Von Guerard Stream 7.4 01/18/2016 42.11 12/31/2015: 9.4 Crescent – East Fork 160 NA 01/08/2017 300 Crescent – West Fork 9.6 01/12/2017 22.79 Green Creek 12.3 163 12/29/2015 41.66 Priscu Stream 28.3 215 01/06/2016 NA Lawson Creek 35.0 260 01/10/2017 13.09

Table 1. Study reaches, reach lengths and sampling dates; mat biomass from the same year transect samples are included, where available.

Methods

Nutrient and tracer additions

To quantify both transient storage and nutrient uptake, we conducted a series of TASCCmethod pulse addition experiments of a conservative tracer (Cl-) and nutrients (NO₃, NH₄ and PO₄) in six streams across the Taylor Valley during the 2015-16 and 2016-17 field seasons. Four of these study streams are located in the Fryxell Basin and two are in the Bonney Basin (see Figure 2). We conducted this series of nutrient-tracer additions once per stream during this study period, with the exception of the study reach on the east fork of Crescent Stream (Crescent East) where we conducted all 3 nutrient additions twice, one time per field season. At each site, three separate nutrient additions were performed sequentially, in this order: NO_3 (as $NaNO_3$), PO_4 (as K_2HPO_4), and NH_4 (as NH_4Cl). A conservative tracer (Cl- as LiCl) was included with each nutrient addition, both to assess transient storage and to enable calculation of solute mass loss for the accompanying nutrient. All three additions were performed on the same day whenever possible; this was logistically necessary for some sites, due to helicopter travel and other constraints, and we standardized this protocol across all sites. All nutrient additions were performed in the middle of the flow season (late December or early January) to ensure that both the hyporheic zone and biota were well-established for that flow season.

The Tracer Additions for Spiraling Curve Characterization [TASCC] method (Covino et al., 2010b) is a pulse addition method that measures nutrient and conservative tracer concentrations along the breakthrough curve. TASCC can estimate whole-stream ambient uptake conditions more accurately than steady-state injections, allowing assessment of stream uptake metrics without added nutrients (Covino et al., 2010a, 2010b). TASCC assumes exponential decline of nutrient concentration with distance downstream and requires accurate assessments of streamflow, channel morphology and sample concentrations. TASCC also allows for calculation of uptake metrics throughout the breakthrough curve, up to saturation; we calculated these values for S_w. Uptake saturation values, while seldom calculated, can provide information regarding stream nutrient uptake capacities and models, and how streams and networks would likely respond to changing nutrient dynamics (Covino et al., 2010a; Earl et al., 2006, O'Brien et al. 2007), e.g. due to land use change, storm pulses, climate changes, and wildland fire or thermokarst inputs.

Using TASCC, the curve for calculated S_w versus total nutrient concentration is regressed to zero added nutrient concentration to determine ambient S_w (Covino et al., 2010b). The shape of this curve also indicates which uptake model biological nutrient processing rates follow, e.g. saturation (Michaelis-Menten), decreased efficiency, or increasing uptake (Figure 1; O'Brien et al., 2007). For the TASCC method, the goal is to reach saturation across all nutrient processing steps (Covino et al. 2010a, 2010b). This informed our decisions re: nutrient salt additions on each reach (Table 2).

Stream	Season conducted	Nutrient addition	Nutrient salt, g	LiCl, g	N or P, g
Crescent East Fork	2015-16	NO ₃ (NaNO ₃)	200	500	32.97
		PO ₄ (K ₂ HPO ₄)	200	500	45.51
		NH ₄ (NH ₄ Cl)	200	500	52.38
Crescent East Fork	2016-17	NO ₃ (NaNO ₃)	200	200	32.97
		PO4 (K ₂ HPO ₄)	200	200	45.51
		NH4 (NH4Cl)	100	200	26.19
Crescent West Fork		NO ₃ (NaNO ₃)	150	100	24.73
	2016-17	PO4 (K ₂ HPO ₄)	150	200	34.14
		NH4 (NH4Cl)	150	200	39.29
Green Creek	2015-16	NO ₃ (NaNO ₃)	300	500	49.45
		PO4 (K ₂ HPO ₄)	300	500	68.27
		NH4 (NH4Cl)	300	500	78.58
Lawson Creek	2016-17	NO ₃ (NaNO ₃)	150	150	24.73
		PO4 (K2HPO4)	200	650	45.51
		NH ₄ (NH ₄ Cl)	200	650	52.38
Drison Stroom	2015-16	NO ₃ (NaNO ₃)	300	500	49.45
Priscu Stream		NO ₃ (b) (NaNO ₃)	200	500	32.97

Table 2. Mass of nutrients and tracer added for each addition experiment

		PO ₄ (K ₂ HPO ₄)	500	1000	113.79
		NH4 (NH4Cl)	300	500	78.58
Von Guerard Stream	2015-16	NO ₃ (NaNO ₃)	300	500	49.45
		PO ₄ (K ₂ HPO ₄)	300	500	68.27
		NH4 (NH4Cl)	300	500	78.58

Nutrient and tracer salts were weighed and added to Ziploc bags in 300g, 200g, 100g and 50g increments. This allowed for flexibility in nutrient and tracer amounts added, based on the varying streamflow conditions for each sampling day and site (see Table 2 for actual masses added). Study reaches were selected to maximize reach length and minimize anabranching and evident surface flow loss from the reach; reach lengths varied from 160-300m (Table 1).

Before each addition, 3-4 background streamwater samples were collected to determine ambient nutrient and tracer concentrations. For each addition, nutrient and conservative tracer salts were thoroughly mixed with streamwater in a 5-gallon bucket to ensure full dissolution. The solute mixture was added at the top of the study reach at a known timepoint (to). All samples, including background, were collected at the bottom of the study reach. At these sampling locations we used specific electrical conductance (SC) sensors (YSI handheld conductivity meter or Campbell Scientific 547 conductance probes) to track the breakthrough of the injected solutes in real time. This helped us determine how frequently to sample as the solute passed the sampling point. We collected approximately 30 samples per addition and attempted to spread these samples evenly across the breakthrough curve. In some instances, the solute pulse passed through more quickly than expected; in these cases, fewer total samples were collected and these were often sparse on the rising limb of the breakthrough curve. Between sequential nutrient additions at a site, downstream SC was monitored in real time and the next addition was not begun until conditions approximated the initial background values, to minimize any carryover of tracer or nutrient from the previous addition. This typically required 1-2 hours. In one case, the Priscu Stream NO₃ addition, a daily flood pulse pushed the solute through very quickly (time to peak = 9 minutes, total time of solute breakthrough was ~16 minutes) and we did not collect enough samples for a clear breakthrough curve; we waited 1.25h until SC approached background and streamflow was more stable, re-ran the NO₃ addition ('NO3(b)' in Table 1), then proceeded with the other two nutrient additions per protocol.

Streamflow measurements are necessary for calculating both uptake metrics and transient storage mass fractions. We measured streamflow before and after each nutrient addition using either a Baski cutthroat flume or SonTek FlowTracker acoustic doppler velocimeter, depending on flow conditions. These are common techniques that the MCM LTER Stream Team uses to measure discharge in these streams. Half of the study reaches were on gaged streams, providing additional streamflow readings at 15-minute intervals. Gaged reaches included Von Guerard Stream, Green Creek, and Lawson Creek. Crescent Stream is gaged below the confluence of the East and West forks, so the gage readings indicate the volume flowing from both channels and cannot distinguish contributions from each fork.

In the field, the stream water samples were kept chilled (4°C) and dark. Within hours, each sample was filtered into three separate HDPE bottles for nutrient, anion, and cation analyses: nutrient samples were filtered through a Whatman G/FC glass microfiber filter, and anion and cation samples were filtered through a NucleporeTM polycarbonate membrane filter with 0.4 mm pore size. After filtration, samples were kept chilled (4°C, anions and cations) or frozen (nutrients) until analysis. Samples were analyzed for nutrient and tracer concentrations following the methods reported in Welch et al. (2010). Nitrile gloves were worn during sample collection, filtration, and analysis to minimize contamination of the samples.

Transient storage mass fraction calculations

To quantify the relative influence of transient storage in each stream, we used a breakthrough curve decomposition model to separate each Cl⁻ breakthrough curve into two mass-fraction compartments: 1) the advection and dispersion mass fraction (approximating a Gaussian distribution of tracer concentration through time), and 2) transient storage mass fraction (Wlostowski et al., 2017). These components are illustrated in Figure 5. Prior to analysis, Cl⁻ samples were background-corrected using the average background sample value for each solute addition. Wlostowski et al.'s (2017) methods include a linear transformation of high-frequency SC measurements collected at the bottom of the reach into modeled 'downstream Cl⁻' concentrations. For most streams, the sampled Cl⁻ data was dense enough that we did not need to perform this transformation. When the samples were too sparse to accurately model the breakthrough curve (e.g., due to very rapid advection, as with Lawson Creek's NO₃ addition), we performed this linear transformation to improve the accuracy of our mass fraction calculations. After calculating the transient storage mass fraction, we tested for geographic influences on transient storage using each stream's distance from the coast as our independent variable.

Nutrient uptake dynamics

We used the TASCC method (Covino et al., 2010b) to estimate ambient nutrient uptake in each study reach. This method calculates uptake length (S_w [L]) and uptake velocity (V_f [L/T]) at each sampling point, providing values through a range of nutrient concentrations, and uses linear transformation to determine ambient S_w and V_f values. For these analyses, sampled nutrient and tracer concentrations were background-corrected using the average background sample concentrations for each nutrient addition, then analyzed per Covino et al. (2010b) to determine S_w and V_f at both ambient and elevated nutrient concentrations. TASCC methods can produce analytical errors associated with low concentrations of the nutrient and conservative solute, e.g. early and late in the solute breakthrough curve, which create noise and negatively impact the assessment of S_w (Finkler et al. 2021). In our samples, this noise was easy to see on visual inspection of the data. If the breakthrough curve tails had 'outlier' values of >2 standard deviations from the plotted S_w vs total nutrient curve, we trimmed the tails to remove noise prior to analysis; this typically removed the first and last 1-2 points (Tim Covino, personal communication, 2021).



Figure 5. Sample breakthrough curve for chloride, with approximate advection-dispersion (red) and transient storage (blue) portions highlighted. The solid line is the Cl- breakthrough curve, while the dashed lines indicate the relative influence of advection-dispersion and transient storage in shaping that curve. Advection and dispersion typically dominate the rising limb and part of the falling limb, while the transient storage fraction peaks in the falling limb.

Microbial mat biomass data

Microbial mat samples have been collected along established transects in MDV streams since 1994 to estimate long-term biomass variation within and across the sample streams. The mats are commonly divided into three categories for biomass assessments, based on dominant color and community composition: orange, green and black (Alger et al., 1997; McKnight et al., 1998). Each type of mat has a different habitat preference, with black, *Nostoc*-dominated mats preferring the wetted margins of streams and orange (*Phormidium* sp. dominated) and green (*Praziolla* sp. dominated) mats preferring submersion in the middle of the channel (Alger et al., 1997; Kohler et al., 2015; Niyogi et al., 1997; Vincent et al., 1993).

Four of our study streams have microbial mat transects: Crescent West, Green, Lawson, and Von Guerard. Our analysis of mat material focuses on these four streams. Mat sampling occurs in January and has been annual since 2002; prior to 2002, these samples were collected approximately every three years. Each sampling visit collects 2-4 plugs of each type of microbial mat near each transect, using a 1.7 cm diameter brass cork borer. These samples are analyzed for AFDM by drying at 100°C for 24 hours, weighing, ashing at 450°C for 4 hours, then re-weighing to determine the mass lost to combustion (Kohler et al., 2015).

This study uses the microbial mat sampling data as an index of benthic mat biomass for each study reach. While these are point samples and do not readily scale to whole-stream biomass measurements, they do allow for comparison across streams. While mat biomass is perennial, it changes from year to year depending on scour and growing conditions that season (Kohler et al. 2015); therefore, we used the data from the same field season as the nutrient uptake experiment (see Table 2 for the uptake addition field seasons). When a stream had more than one mat transect (e.g. Von Guerard), we used the one closest to our study reach. We expect biomass to correlate with higher nutrient uptake rates (smaller S_w and larger V_f values); we also expect this relationship will be stronger in streams with lower transient storage, as this would indicate a greater influence of in-channel processes.

Data analysis – controls on nutrient uptake

We used simple linear regressions (in base R) to assess the influence of potential controls on nutrient uptake dynamics, testing both S_w and V_f for relationships. To assess the influence of microbial mat standing stock on nutrient uptake dynamics, our independent variable was 1) the average microbial mat biomass for our study season and 2) the average chl-a for our study season. Because mats in the wetted channel (orange and green) may influence uptake more strongly than mats on the wetted margins (black), we also looked for relationships between the spiraling metrics and these location-based channel and edge mat groups. To determine whether the geographic N:P gradient influenced either of the uptake metrics, our independent variable was distance from the coast. To assess the influence of transient storage on nutrient uptake dynamics, we used the calculated transient storage mass fraction for each stream as the independent variable. We also performed a Kruskal-Wallis test to determine whether any nutrient species (NO₃, NH₄, PO₄) had a significantly different transient storage mass fraction. Kruskal-Wallis was appropriate for the latter analysis because the sample size was small (n = 7)and the data were not normally distributed. All analyses were performed in R (R Core Team (2021), version 4.1.0, "Camp Pontanezen") using the "stats" package in base R.

Results

Transient storage mass fraction

The transient storage mass fraction for the Cl⁻ breakthrough curves was similar for most streams and nutrients, and ranged from 0.14-0.48 with a median value of 0.19 (Figure 6). These can be interpreted as proportions of solute mass (and mass-labeled water) that occupied transient storage for an appreciable time, compared to the timescale of advection and dispersion. Lawson Creek had a higher transient storage mass fraction than other study streams for both NH₄ and PO₄, but there were no significant differences in transient storage either by nutrient or by geographic location (all p > 0.05). The transient storage model failed for Lawson Creek's NO₃ addition, both with and without the SC modeling to improve point density.



Mass Fractions: Advection-Dispersion and Transient Storage

Figure 6: Mass fraction of the advection-dispersion (AD) and transient storage (TS) components for each Cl- breakthrough curve, ordererd by stream and nutrient. CE = Crescent East, CW = Crescent West, and VG = Von Guerard. The transient storage model failed for Lawson's NO₃ data both with and without the SC modeling.

TASCC nutrient uptake dynamics

We were able to calculate ambient S_w and V_f values for all nutrients and study streams (Table 3). While uptake metrics did vary by nutrient, especially for S_w , they were fairly similar for V_f (Figure 7). This indicates relatively similar uptake across reaches and nutrients, as V_f accounts for differences in stream width, depth, discharge, and velocity. For NO₃-N, ambient S_w ranged from 1.54-1503 m and ambient V_f ranged from 0.0061-105 mm/min; for PO₄-P, ambient S_w ranged from 55-670 m and ambient V_f ranged from 0.038-7.48 mm/min; and for NH₄, ambient S_w ranged from 83-254 m and ambient V_f ranged from 0.02-7.63 mm/min. MDV S_w and V_f values are comparable to those found in other stream systems (Figure 8).

Stars and	National	Ambient S _w	Ambient V _f
Stream	nuirieni	<i>(m)</i>	(mm/min)
	NO ₃	940	0.31
Von Guerard	PO ₄	511	1.04
	NH_4	254	1.98
	NO ₃	884	0.01
Crescent East - 1516	PO ₄	55	0.04
	NH4	106	0.01
	NO ₃	1503	0.10
Crescent East - 1617	PO ₄	346	0.20
	NH4	130	0.37
	NO ₃	1.54	104
Crescent West	PO ₄	670	0.13
	NH4	109	0.56
	NO ₃	47	9.14
Green	PO ₄	261	1.79

Table 3. Ambient S_w and V_f by stream and nutrient

	NH4	124	3.51
	NO ₃	378	3.36
Priscu	PO ₄	162	7.48
	NH ₄	157	7.63
	NO ₃	469	0.21
Lawson	PO ₄	109	0.80
	NH4	83	0.68



Nutrient uptake velocities in study streams



Figure 7: Boxplots of ambient uptake lengths (S_w) and velocities (V_f) by nutrient addition. Colored dots are the actual datapoints for added transparency. The y-axis on the V_f plot was rescaled for improved data visualization. One datapoint (NO₃ $V_f = 104$) is not visible with this rescaling.



Figure 8. Uptake length (S_w) at different streamflow levels for MDV NO₃(A), PO₄ (B) and NH₄ (C), compared to results from a meta-analysis of other streams (dataset from Hall et al., 2013). MDV stream points are in red. The compilation dataset includes large streams with flow rates up to 5K L/s. We adjusted the x-axes for better visualization of the studies at lower flows, which are most comparable with ours. A parallel comparison for V_f yielded similar results.

We also calculated spiraling metrics across the nutrient breakthrough curve to determine uptake kinetic models for each stream and nutrient. Per O'Brien et al. (2007), when a saturation or Michaelis-Menten relationship exists, S_w will increase steadily as total nutrient concentration increases (Figure 1a). This occurred in most of our reaches (see supplemental information for all Sw-nutrient curves). With a 'decreased efficiency' relationship, per Mulholland et al. (2002) and others, the S_w-total nutrient curve is hyperbolic (Figure 1a). This appears to occur in Crescent East NO₃ for both study years, and also in Crescent West PO₄. We also saw the third model, where uptake rates appear to increase with increasing concentration, and found both linear (first order) and non-linear (biostimulation) dynamics. With a 1st order relationship, where processing rates increase with concentration, the S_w-total nutrient plot appears flat or chemostatic (Figure 1a). This occurred in the Green Creek PO₄ addition and the Priscu Stream NH₄ addition. We also see a biostimulation model, where Sw steadily decreases and Vf increases as nutrient concentration increases, indicating a greater than 1st order (perhaps exponential) increase in biological nutrient processing as concentration increases. This occurred strongly in Von Guerard Stream PO₄, and to a lesser extent in Crescent East 1516 PO₄.

We also observed hysteretic uptake behavior in the S_w-total nutrient concentration relationship. This S_w behavior would be mirrored by the nutrient-V_f relationship; e.g. an addition with clockwise S_w hysteresis would also have counterclockwise V_f hysteresis. This has been reported in other TASCC uptake studies: the rising limb is commonly interpreted as representing the influence of advection-dispersion processes on uptake dynamics, while the falling limb indicates the influence of transient storage processes (Finkler et al., 2021; Gibson et al., 2015; Rodriguez-Cardona et al., 2016). In MDV streams, this translates to the influence of in-channel (rising limb) vs. hyporheic (falling limb) processes on nutrient uptake. We found general patterns to the S_w-nutrient hysteresis, which differed by nutrient (Figure 9). For NO₃, most streams did not have S_w-nutrient hysteresis; the exception was Von Guerard Stream, which showed clockwise hysteresis, indicating faster uptake on the falling limb and a stronger influence of hyporheic versus in-channel processes on NO₃ uptake. For PO₄, most streams showed clockwise hysteresis, again indicating a strong transient storage influence on uptake. The exceptions here were Crescent West, which did not have S_w-nutrient hysteresis, and Priscu Stream, which showed counterclockwise hysteresis, indicating a greater influence of in-channel processes. For NH₄, most streams showed counterclockwise hysteresis, indicating a greater influence on inchannel processes on NH₄ uptake. Exceptions were Priscu Stream, where uptake remained the same across the breakthrough curve, and Lawson Creek, which showed clockwise hysteresis and a greater influence of hyporheic processes.

On Crescent West, we observed a lagged NO₃ pulse during the NH₄ nutrient addition (Figure 10). This is similar to findings in an oligotrophic Arctic stream (Snyder & Bowden, 2014) and indicates that hyporheic nitrification is occurring rapidly in this system: NO₃ began to rise 24 minutes into the NH₄ addition, and dropped back to ambient levels just over an hour from to. Integrating under the breakthrough curve, the total mass of NO₃ in this pulse was calculated to be 34 mg. Other streams, including Crescent East, showed some elevation of NO₃ concentrations in the tail of their NH₄ addition, but these signals were very close to detection limits and not as clear as the Crescent West pulse.



Figure 9: Typical S_w-nutrient behavior for each nutrient addition. NO₃ was the most similar between rising and falling limbs of the solute breakthrough curve; PO₄ tended to show clockwise hysteresis; and NH₄ tended to show counter-clockwise hysteresis. Shorter values for S_w are linked to faster uptake.



Figure 10. For Crescent West, a lagged NO₃ nutrient pulse was measured during the NH₄ nutrient addition; the NO₃ pulse peaks about 60 seconds after the NH₄ pulse. The dashed black line is the NH₄-N that we would expect under 100% conservative transport. The solid black line is the NH₄-N observed in our samples. The grey line is the NO₃-N we observed during the NH₄ nutrient addition. The total mass of observed NO₃-N in this pulse was 34 mg.

Comparisons between streams

We found few significant results (i.e. p < 0.05) when testing for the various controls on uptake metrics across streams. When testing mat biomass [AFDM] as a control on spiraling metrics, we found two significant relationships: between black (wetted edge) mat AFDM and S_w for NH4 additions (Figure 11a), and channel mat (orange+green) AFDM and V_f for PO4 additions (Figure 11b). There were no significant relationships for other nutrients or mat combinations, and there were no significant relationships between either spiraling metric and mat *chl-a*. There were also no significant relationships between V_f or S_w and: geographic location along the nutrient gradient (Figure 12); ambient nutrient concentrations (Figure 13a); transient storage (Figure 13b); or the ratio of N uptake to P uptake (all p > 0.05).



Figure 11. Assessing the influence of AFDM on spiraling metrics, the two significant relationships were for S_w and black mat AFDM (a; p = 0.038, $R^2 = 0.99$) and for V_f and channel mat AFDM (b; p = 0.015, $R^2 = 0.89$). 'Channel mat' includes both orange and green mat biomass; these mats live in the stream channel. Black mats live on the wetted margins of streams.



Figure 12. S_w (a) and V_f (b) by distance from coast, which corresponds to location along the geographic N:P gradient. Points are colored by nutrient addition. For S_w , the NH₄ point for Priscu Stream (28.3 km from the coast, $S_w = 7.63$) is obscured by the PO₄ point ($S_w = 7.48$). The V_f y-axis was rescaled to 15, to better visualize most of the datapoints. There is one additional V_f point, for Crescent West NO₃ (9.6 km from the coast), $V_f = 104.7$, which is not visible with this rescaling.



Figure 13. Linear regressions of S_w against ambient nutrient concentrations (a) and the transient storage mass fraction (b) for each nutrient addition experiment. Points are colored by nutrient type. The plots of V_f against ambient nutrient concentrations and against transient storage mass fractions look very similar to these S_w plots. None of these relationships are significant (all p > 0.05). For (a), R^2 values ranged from 0.01-0.17. For (b), NH₄ had an R^2 value = 0.5; all other R^2 were < 0.3.

Discussion

Site selection:

This study spanned the Taylor Valley, with sites in both the Fryxell and Bonney basins. Ideally, we would have included a study site in the Lake Hoare basin, but this was not logistically feasible. There were no suitable streams in the Hoare basin: there are only two with dependable flow; of these, one is too short for an uptake experiment, and the other flows next to its source glacier for most of its length. As a result, when the latter stream is flowing there are multiple water inputs along the length of the stream, changing both the discharge and background water chemistry. This violates the assumptions of the TASCC method and would pose strong challenges to any uptake method.

Transient storage mass fraction

The transient storage fraction, i.e. the proportion of conservative tracer (and water) mass delayed by transient storage, averaged around 0.22 across all study streams and was as high as 0.48. This indicates that over 1/5 of the nutrient solute was also moving through hyporheic flowpaths and interacting with hyporheic biota and substrates. These findings support other MDV studies regarding the porous and well-connected hyporheic zones (e.g. Cozzetto et al., 2013; Gooseff et al., 2002), as well as the importance of hyporheic processes in nutrient uptake and transformation (Gooseff et al., 2004; Koch et al., 2010; McKnight et al., 2004). It is likely that many of these transient storage values are underestimates, because we were seldom able to capture the full tail of the breakthrough curves due to sampling logistics and time constraints. Therefore, the actual transient storage mass fractions are probably somewhat higher across all streams. Most of our streams have very similar transient storage mass fractions; this is due to the timing and nature of our uptake studies. While transient storage does vary in these streams, depending on both active layer depth and flow conditions (Conovitz et al., 2006), these conditions were fairly uniform in our late-season study windows.

TASCC nutrient uptake dynamics

MDV ambient V_f and S_w values are similar to those found in temperate, boral and arctic streams (Figure 8); while V_f is generally considered more appropriate for comparing uptake across this broad collection of streams, since it accounts for variations in water depth and velocity, far more studies have reported S_w and we used this metric to enable the broader comparison. Plotting S_w versus streamflow controls for these differences. The plots of V_f and discharge for each nutrient look very similar to the ones shown for S_w , just with far fewer data points. Tank et al. (2008) conducted a meta-analysis of uptake results for NO₃ and NH₄ from other studies in temperate streams. In this compilation, V_f values for NO₃ ranged from 0.02-1790.33 mm/min, with a median of 3.06; V_f values for NH₄ ranged from 0.27-119.4 mm/min, with a median value of 4.07. Hall et al. (2013) compiled uptake results for PO₄, and their supplemental dataset shows V_f values ranging from 0.03-11.65 mm/min with a median value of 1.44.

Most of our nutrient additions followed accepted models of uptake kinetics (see Figure 1): saturation (Michaelis-Menten) and decreasing efficiency (Covino et al., 2010b; Dodds et al., 2002; Mulholland et al., 2002). Four additions showed increasing uptake as concentration increased. Green Creek PO4 and Priscu Stream NH4 had a 1st order (linear increase) kinetic response to increased concentrations, indicating a steady increase in nutrient processing rates with increased concentrations (no saturation). This lack of evident saturation could indicate that not enough nutrient was added to reach saturation; but since the maximum pulse of added nutrients were well above ambient concentrations (by > 2 orders of magnitude), this seems unlikely. In these instances, it may indicate a high demand for the nutrient. Von Guerard Stream PO₄ and Crescent East 1516 PO₄ had a 'biostimulation' response (Diemer et al, 2015) with strongly (roughly exponentially) increasing nutrient processing rates with increasing concentrations. This uptake response has been observed in streams with chronically-high nutrient loads (Covino et al., 2012) and a watershed history of wildfire disturbance (Diemer et al., 2015). These explanations do not fit MDV streams, with their low ambient concentrations for all nutrients (Figure 3) and lack of both vegetation and wildfire disturbance. In streams with low ambient nutrient concentrations, both Diemer et al. (2015) and Rodriguez-Cardona et al. (2016) suggested this biostimulation response may be a form of 'priming effect', as described in soil

microbial literature (Blagodatskaya & Kuzyakov, 2008): i.e., accelerated microbial activity in response to a soil treatment. This 'priming' treatment is usually an organic carbon addition but could also be a response to the high nutrient concentrations used in a TASCC nutrient addition.

There were many instances where MDV streams continued to process all three nutrients, even at greatly increased background concentrations (thus exhibiting either the efficiency loss, 1st order or biostimulation model). This indicates that, in spite of the harsh climate and short growing season, MDV stream biota are able to retain nutrients at and above the current ambient levels. Current MCM LTER hypotheses predict that a warming East Antarctic will result in wetter and more connected ecosystems, with resulting higher nutrient loading in streams and lakes. Our results indicate that existing biota may be capable of keeping pace with these projected increases in nutrient loading. This accelerated biotic uptake and retention could prevent elevated nutrient loads from entering the closed-basin terminal lakes via the stream channels.

Our results for Vf show that when we account for size and flow differences, MDV streams have similar nutrient uptake rates across the valley, regardless of background concentrations and N:P ratios (Figure 7). The most notable difference between the nutrient additions was the nutrient-dependent patterns of Sw-total nutrient hysteresis across the breakthrough curve (Figure 1), which indicate the degree of in-channel versus hyporheic processes impacting uptake (Finkler et al., 2021; Gibson et al., 2015; Rodriguez-Cardona et al., 2016). Most of our study streams followed this pattern: NO₃ uptake had balanced in-channel and hyporheic influences (no Sw hysteresis); PO4 uptake was dominated by hyporheic processes (clockwise Sw hysteresis); and NH4 uptake was dominated by in-channel processes (counterclockwise Sw hysteresis). Note that while one set of processes may have relative dominance in different additions, N and P uptake demonstrably occur in both the channels and

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hyporheic zones of these streams. (Gooseff et al., 2004; Koch et al., 2010; McKnight et al., 2004). These results further demonstrate the importance of the hyporheic zone in stream biogeochemical processes.

We saw evidence of rapid nitrification in Crescent West (Figure 10). Other reaches, including Crescent East, had measurable NO₃ in the tail of their NH₄ addition but no distinct NO₃ pulse, perhaps due to the very low NO₃ levels measured (near detection limit). Crescent West was our longest reach (300m), and MDV stream length is correlated with hyporheic influence (Singley et al., 2017; Wlostowski et al., 2018). Thus, we may have seen a stronger nitrification signal in other streams if they had longer reaches and therefore greater net hyporheic residence time. This hypothesis is supported by the findings of Singley et al. (2021), who found evidence for hyporheic nitrification of desorbed NH₄; while their findings are complemented by our evidence of dynamic NH₄ uptake and nitrification on a sub-hourly timescale.

In Fryxell basin streams, median N:P ratios range from 2.7 to 6.4, while Bonney basin streams have median N:P ratios of 34.7 to 94.7 (Figure 4). Uptake dynamics are not influenced by this range of N:P ratios (Figure 11). However, there are biotic patterns related to this ratio: Barrett et al. (2007) demonstrated that microbial mat presence is linked to lower N:P ratios in streamwater. Because these mats have N:P ratios close to the Redfield ratio of 16:1 (Barrett et al. 2007), this implies that microbial mats are key controls on ambient nutrient concentrations in streams. This is supported by other evidence of NO₃ uptake and transformation in microbial mats (Gooseff et al., 2004; McKnight et al. 2004). Hyporheic zones are known sites of nutrient uptake and transformation in MDV streams (NO₃, Koch et al. 2010; NH₄, Singley et al. 2021), thus hyporheic biofilms may also influence instream ambient nutrient concentrations.

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The uptake metrics we found in our streams are similar to those found in other studies, both in the MDV (Gooseff et al., 2004) and other biomes (Hall et al., 2013; Figure 8). This similarity to streams in other biomes is surprising because of the relatively short active season for MDV biota (e.g., McKnight et al., 1999) and low levels of organic carbon (Torrens et al., 2022) and nutrients (Welch et al., 2010) in these streams. This, together with the steady or increasing uptake observed for some nutrients and sites throughout the breakthrough curve, indicates that MDV biota can effectively respond to and assimilate nutrients at concentrations far higher than ambient. This has implications for their resilience as the Antarctic climate warms and melts, increasing nutrient mobilization and altering the current baselines.

Nutrient spiraling methods are not able to distinguish between instream and hyporheic uptake, which we address with our analysis of transient storage mass fraction. They also do not distinguish between biotic and abiotic 'uptake', or removal, of nutrients from the water column. This is a particular issue for PO₄ and NH₄ additions, as these compounds are readily sorbed to the substrate. Our results, including the NO₃ pulse on Crescent West and the PO₄ correlations to orange and black mat biomass, suggest a stronger biological control than sorption. This is supported by with mesocosm and tracer studies that showed biological PO₄ uptake (Kohler et al., 2016; McKnight et al., 2004). However, we are not able to quantify the relative amounts of biotic and abiotic uptake from this study. While nutrient spiraling methods do not differentiate between biotic and abiotic removal, it is possible to determine this with other methods. Munn & Meyer (1990) used laboratory studies of stream sediments to assess the influence of biotic versus abiotic removal. The accuracy of future uptake studies would be improved by incorporating these or similar methods to distinguish the amounts of biotic and physical removal that occur.

Controls on nutrient uptake

We hypothesized that the amount of mat biomass, transient storage, or ambient concentrations (e.g. location along the N:P gradient) would influence nutrient uptake in MDV streams. We did not find evidence for any of these as controls on MDV nutrient uptake. Other studies have found that microbial mat biomass influences nutrient uptake (Bernhardt et al., 2003, 2005; Harvey et al., 2003; Marti et al., 1996), which does make intuitive sense. The MCM LTER microbial mat data are point samples, which do not readily scale to whole-stream biomass measurements. We may have found a different result if we had more accurate whole-stream biomass values for the sampling sites and seasons. There was no relationship with uptake and transient storage, as our calculated transient storage mass fraction was similar across most streams. This is likely due to the timing of these nutrient additions: all additions occurred in the middle to late part of the flow season and while flow was actively occurring, which means that all hyporheic zones would be more or less at their full seasonal extent (Conovitz et al., 2006).

While there was not a significant relationship between the calculated transient storage mass fraction and any uptake dynamic, it is clear that hyporheic processes are important for nutrient uptake and transformation: approximately 22-48% of added nutrients (22-48% of added solute) flowed through the hyporheic zone during each addition, indicating strong potential for hypotheic influence; hyporheic processes were dominant in many additions; and hyporheic nitrification is demonstrated in Crescent West.

Although nutrient concentrations are known to influence uptake dynamics (e.g. Mulholland et al., 2002) and higher existing background levels may increase overall uptake (e.g. Dodds et al., 2002; O'Brien et al. 2007), we did not find an apparent pattern to uptake based on ambient concentrations. We did find multiple instances where uptake kinetics did not saturate,

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but continued to increase as nutrient concentrations increased more than two orders of magnitude above ambient. These responses ranged from moderate increases (the 'decreased efficiency' model) through linear increases (the 'first order') model and even included some exponential or biostimulation responses, indicating that biotic nutrient processing can accommodate much higher nutrient loads than these streams currently carry.

Conclusions

This study is the first to quantify MDV stream uptake dynamics for NH4, and the first to quantify NO₃ and PO₄ on this geographic scale. In spite of the harsh climate, short growing season, and low levels of nutrients and organic carbon in this ecosystem, our uptake metrics are similar to those found in temperate streams for all three nutrients. This may be due to the relatively high standing stock of algal biomass in the MDV, where, unlike in temperate streams, there is no invertebrate grazing to act as a control on algal biomass. We did not find evidence for nutrient uptake patterns based on geographic differences in ambient nutrient concentrations (including the MDV's geographic N:P ratio), perhaps because these concentrations are very low across the valley and the gradient was not great enough to generate differences in nutrient demand. We show that the hyporheic uptake component is important for all three nutrients, which supports Koch et al.'s (2010) and Runkel's (2007) findings for hyporheic NO₃ processing and expands it to NH4 and PO4. Crescent West results provide dynamic evidence of rapid hyporheic nitrification in these streams. These findings of rapid NH₄ uptake and transformation are another line of evidence of high biotic demand for NH4 (also see Singley et al., 2021), which may explain the extremely low ambient NH4 concentrations in most streams (near or below detection limit), and the extensive supply of NO₃ in the hyporheic zones of these streams

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(Singley et al., 2021). Our results also indicate that MDV stream biota have the capacity to assimilate and transform nutrients both at and well above current ambient limits. This finding has implications for projected climate warming changes to this landscape, where a warmer, wetter and more connected ecosystem is predicted; MDV stream biota may be able to thrive under the projected changes, as well as reduce or prevent increased nutrient loading to the terminal lakes via stream channels.

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Chapter IV

Disturbance and resilience in a harsh environment: stream biological response to thermokarst activity in the McMurdo Dry Valleys, Antarctica

Abstract

Climate warming has impacted stream ecosystems on a global scale. In permafrost regions, these impacts include thermokarst development, e.g. land subsidence due to permafrost thaw. When this occurs near streams, it increases stream sediment and nutrient loads by orders of magnitude, impacting downstream hydrology and ecology. Thermokarst is a major driver of landscape change in the Arctic, but few studies have addressed its impacts in Antarctica. This study examines the biotic impact of a 2012 thermokarst development in Crescent West, a glacial meltwater stream in the McMurdo Dry Valleys (MDV), Antarctica. We know this event caused changes to the stream channel geomorphology, substrate, and nutrient loads. We do not know how the biota, predominantly microbial mats, have responded to this disturbance. Two factors have contributed to this lack of information: mat biomass change has been studied on a transect (established 2013), but we have not had a scalable method of assessing landscape-scale biotic change; and we do not have data on biota from this reach of Crescent West prior to 2012. To overcome these issues, we used remote sensing imagery and analysis to assess biotic coverage above and below the thermokarst origin. We calculated changes in areal biotic coverage for the period from 2010-2019, to capture both the immediate and longer-term biological response. We also assessed biotic coverage in three nearby stream channels, to control for basin-scale changes. We found no evidence of decreased biotic cover due to the thermokarst development. Instead, biotic cover rose in both the impacted reach and across the basin in 2013. This indicates the

influence of some other basin-scale covariable that season; it is also a testament to the resilience of the microbial mats in this polar desert. This study is one of few to explore ecosystem response to disturbance in these streams, and the first to examine MDV disturbance dynamics using remote sensing techniques.

Introduction

Stream ecosystem disturbance due to anthropogenic climate change is a global concern (Carpenter et al., 1992; Palmer et al., 2008). Climate-related impacts to stream ecosystems can include flooding, drying or increased intermittence of streams, increased wildfire impacts, streambank erosion or subsidence, and related changes to watershed nutrient and carbon cycling and transport. These in turn impact ecological communities, human infrastructure, water quality and more (e.g., Palmer et al. 2008). At the poles, both the Arctic and the Antarctic have experienced amplified climate changes in the last decades, triggering physical and biological shifts in terrestrial, marine and freshwater ecosystems (Bromwich et al., 2013; Chapman & Walsh, 2007; Hinzman et al., 2005; McClintock et al., 2008; Post et al., 2009; Steig et al., 2009).

While East Antarctica has experienced climate-related changes (IMBIE Team, 2018; Steig et al., 2009), there has not been a warming trend in the McMurdo Dry Valleys (MDVs), located on the Ross Sea in East Antarctica (Obryk et al., 2020). However, this region has experienced multiple disturbances that may be precursors of increased warming and enhanced ecosystem connectivity, including heat waves, floods, rising lake levels, and both permafrost and lake ice thaw (Gooseff et al., 2017). The 2001-02 'flood year', caused by a climate anomaly where unusually high summer temperatures coincided with high solar fluxes (Doran et al. 2008), was a pivot point for this ecosystem; widespread melt and flooding caused immediate and longterm changes to both physical and biological ecosystem components, which persist long after the initial disturbance has receded (Gooseff et al., 2016, 2017). The physical changes to the landscape, including changes to stream flow, channel morphology, and substrate composition, tended to be immediate, while many biological responses lagged by 1-5 seasons. This lagged biological response to physical change is not uncommon (Gherardi & Sala, 2015), and may occur if the physical drivers and population growth rates or turnover times operate on different timescales (Bestelmeyer et al., 2011; Kohler et al., 2015a; Overhoff et al., 1993). It is expected that climate change impacts will increase in the MDVs in coming decades (Gooseff et al. 2016, 2017), and associated increased wetness and ecosystem connectivity will be a hallmark of future, warmer years (Chapman & Walsh, 2007), adding urgency to any study of MDV ecosystem response to disturbance.

Thermokarst development, or the subsidence of land due to thawing permafrost, is a major driver of climate-related landscape change in the Arctic (Hinzman et al, 2005). Thermokarst slumps can cause dramatic changes to landscape morphology (Hinzman et al., 2005; Kokelj et al. 2013). If this subsidence occurs adjacent to a stream, it can increase stream sediment and nutrient loading by several orders of magnitude (Bowden et al., 2008; Kokelj et al. 2013), impacting water chemistry and aquatic ecosystems. In January 2012, researchers discovered a thermokarst-impacted area in the west fork of Crescent Stream (Crescent West; Gooseff et al., 2016; Sudman et al., 2017; see supplemental figure S4.1); there were no parallel impacts in the east fork (Crescent East). Monitoring of Crescent Stream (for more than 2 decades) occurs at and near the stream gage box, which is 500 m below the confluence of the two forks; thus little is known about Crescent West's biological or physical conditions before the thermokarst development (Gooseff et al., 2016). Post-subsidence, physical changes have been

well-documented, and include changes to stream morphology, fining of the substrate, intermittently-increased sediment loading and TSS (total suspended solids), and increased streamwater concentrations of nitrate and other ions (Gooseff et al., 2016; Sudman et al., 2017). These physical changes have implications for the biological communities, but less is known about these biological impacts.

The primary drivers of MDV stream ecosystem function are benthic microbial mats and hyporheic biofilms. We know these biota are adapted to the MDV's harsh polar desert conditions, which include months of total darkness in winter, a mean annual temperature of -19° C, and less than 50 mm annual precipitation (Doran et al. 2002; Fountain et al. 2010). Growth and production are limited to short summer growing seasons of 4-9 weeks, when streams are flowing (Wlostowski et al., 2016). Even these summer periods are harsh, and are characterized by punishing radiative inputs, strong diel flood pulses, no-flow periods (Wlostowski et al., 2016), and low levels of nutrients and carbon (Welch et al., 2010; Torrens et al., 2022). The microbial mats overwinter as freeze-dried crusts and can reactivate within 20 minutes of rehydration (Vincent & Howard-Williams, 1986). They have pigmentation (scytonemin) that provides protection from the intense summer UV rays (Vincent et al., 1993). Their preferred habitat is stream reaches with stable desert pavement substrate (McKnight et al., 1999) and low sediment loads (Vincent & Howard-Williams, 1986), where they form thick perennial colonies. They tend not to colonize reaches with unstable, shifting, sandy sediments that can generate high sediment loads at higher flows (Alger et al., 1997). Grazing impacts here are negligible (Treonis et al., 1999); the primary checks on microbial mat growth are flow conditions (Kohler et al., 2015b; McKnight et al., 1999) and scour from the diel flood pulses (Cullis et al., 2014; Kohler et al.

2015a). We do not know how these microbial communities will respond to changing conditions associated with climate warming.

There have been few MDV studies on stream ecosystem response to disturbance (but see Kohler et al., 2015a; McKnight et al., 2007). We know these mats are sensitive to scour and that they may require multiple seasons to regain scoured biomass (Kohler et al., 2015a). Thus they may be negatively impacted by the physical impacts of thermokarst development and associated loading of fine sediment into streams (Sudman et al., 2017). Conversely, the microbial communities in the stream and hyporheic zone recover quickly from some disturbances (e.g. a decade without water; McKnight et al, 2007) and may benefit from the increased nutrient loading that accompanied subsidence (Gooseff et al., 2016). After the Crescent West thermokarst zone was discovered, MCM LTER researchers established a transect for sampling microbial mats below the thermokarst site, to monitor changes to mat communities in the years after the subsidence (McKnight, 2019). While this study transect provides useful information, it has two drawbacks: first, it is a point sample that does not necessarily capture or scale to whole-stream biotic changes, given the inherent patchy distribution of MDV microbial mats (Kohler et al., 2015b); and second, there is a lack of pre-thermokarst data for comparison. The overall lack of pre-thermokarst data has hindered assessment of the biotic response to the Crescent West thermokarst disturbance; in this study, we use remote sensing analyses to remove this impediment.

Recent MDV studies have used remote sensing imagery and analyses to assess microbial mat cover across Taylor Valley (Power et al., 2020; Salvatore et al. 2020, 2021). Remote sensing and image analysis can provide long-term, spatially broad estimates of biomass and primary production, which makes them well-suited to remote areas. Remote sensing can detect

photosynthetic biomass and productivity because chlorophyll-a (chl-a) has a strong and unique spectral signature of absorbance in visible wavelengths and reflectance in the near-infrared spectrum. This signature, also known as the 'red edge' (Collins, 1978), is the basis for vegetation indices such as the normalized difference vegetation index [NDVI]. These vegetation indices have been used to derive vegetation properties including biomass, composition, photosynthetic activity, and health, most notably in forestry and agricultural applications (Mulla, 2013; Xue & Su, 2017). NDVI is versatile and can be used to identify a broad range of photosynthetic pigments. In MDV microbial mats, scytonemin is a dominant pigment, with concentrations approximately an order of magnitude higher than that of chl-a (Vincent, 1993); it acts as 'microbial sunscreen', protecting mats from UV radiation, and is commonly found in terrestrial mats exposed to extreme environments where protection from UV radiation is paramount (Garcia-Pichel & Castenholz, 1991). Like most other photosynthetic and sunscreen pigments, scytonemin is strongly absorbing at visible wavelengths and poorly absorbing at near-infrared wavelengths, respectively. Collectively, these pigments have been correlated with biomass and primary productivity measurements in the Canada Glacier Antarctic Special Protected Area (Power et al. 2020; Salvatore et al. 2020).

The goal of this study is to use remote sensing and spectral parameter-based analyses to quantify microbial mat areal cover in Crescent West a) before and after the 2012 thermokarst development and b) above and below the upper boundary of the thermokarst development (Sudman et al., 2017), to determine whether there is a detectable thermokarst-induced change to the microbial mat extent. We expect to find an immediate decline in downstream biotic activity after the thermokarst development, due to the scouring or burial of microbial mats; then a longer-term recovery or increase in downstream mat areal cover in response to elevated nutrient loads

that accompany thermokarst subsidence. We will also use this technique to assess whole-stream mat coverage over time in three other nearby MDV streams: Crescent East, Green Creek, and Von Guerard Stream. This will help to identify any broader, valley-wide trends in mat areal cover, distinguishing them from thermokarst-related change. It will also provide a more comprehensive view of annual microbial mat cover than has previously been available.

Methods

Site description

To assess changes in whole-stream microbial biomass over time, we performed our analyses on four stream reaches: Crescent East, Crescent West, Von Guerard Stream, and Green Creek (Figure 1). To test for thermokarst-related changes within Crescent West, we also analyzed this reach above and below the upper boundary of the thermokarst development (as recorded by Sudman et al., 2017). In this chapter, we refer to the area above the thermokarst activity as "upper Crescent West" and the area below the activity as "lower Crescent West". For all analyses (field data, remote sensing), we have chosen to evaluate the period 2009-2019 (i.e., the 2009-10 austral summer to the 2018-19 austral summer). This provides a few years of data prior to the thermokarst occurrence (early January 2012) and ample post-thermokarst time to evaluate potential recovery.

The intermittent glacial meltwater streams of the MDVs have relatively simple hydrology and biology. They flow 4-9 weeks per year during the austral summer (McKnight et al., 2004; Wlostowski et al., 2016), through permafrost-bounded glacial alluvium (Gooseff et al., 2011). MDV stream channels tend to be oversized such that streamflow seldom fill the entire channel width; thus, the bed width can be several times larger than the wetted width, and anabranching

across the streambed is common, especially at moderate to low gradients (Koch et al. 2011). Streamflow varies on diel and seasonal cycles and is characterized by daily flood pulses, which can quickly raise the streamflow by an order of magnitude (Conovitz et al., 1998). There are no macrofauna or vascular plants in this system; perennial, benthic microbial mats and hyporheic biofilms drive stream ecosystem function (Hawes & Howard-Williams, 1998; McKnight et al., 1999). Microbial mats also dominate stream biomass (Hawes & Howard-Williams, 1998; Kohler et al., 2015b), and have been sampled on established transects since 1994 (McKnight, 2019; see 'Microbial Mat Sampling' in this Methods section for more details).



Figure 1: Map of Fryxell Basin, MDV with our study streams highlighted. Gage box locations are marked in white and microbial mat sampling transects are marked in orange.

Satellite imagery and processing

Multiple WorldView-2 [WV02] 8-band multispectral satellite images (DigitalGlobe, Inc.) covering our study areas (Crescent Stream, Green Creek and Von Guerard Stream) over a timespan from 2010-2019 (e.g. before and after the 2012 thermokarst development) were acquired from the Polar Geospatial Center (PGC) through a cooperative agreement between the National Science Foundation and the National Geospatial Intelligence Agency. Images were ordered from the PGC as orthorectified top-of-atmosphere reflectance data, with the technique shown to result in geographic accuracies on the order of 1-2 pixels (1-8m; Aguilar et al., 2013). For each study year, one clear, cloud-free image was selected from January or early February, to approximately coincide with the timing of microbial mat transect sampling. No high-quality, cloud-free images of our target sites were acquired for all of 2016, due to persistent cloud cover observed in all available data; 2016 was therefore omitted from our remote sensing analysis. Once selected, spectral contributions from Earth's atmosphere were removed from each image using the ENVI image processing software and methods described in Salvatore et al. (2015) and Salvatore et al. (2020). Atmospheric corrections were generated using five invariant in situ geologic surfaces that were spectrally characterized during the 2018-19 field campaign in Taylor Valley. Regression lines were generated for each band between the ground-based surface and orbital top-of-atmospheric observations, allowing for the use of ground-validated spectra to ensure comparability between images. This method provides a higher level of validation than the scene-derived atmospheric correction techniques used in many earlier MDV remote sensing studies (Power et al., 2020; Salvatore et al., 2014; Salvatore et al., 2015; Salvatore et al., 2020), and is more appropriate for this study's broad-scale, satellite-based quantitative analyses.

After calibration to surface reflectance, each 8-band WV02 pixel was unmixed using a linear least squares regression model (Ramsey & Christensen, 1998), the methods described in Salvatore et al. (2021), and the endmember library detailed in Table 1. This technique linearly combines a series of endmember library spectra to best match the observed sample spectrum with the least amount of residual offset (measured as the root mean square (RMS) error). The assumption of linear mixing is not often adopted for visible and near-infrared spectral investigations, but Salvatore et al. (2020; 2021) demonstrate the optical opacity of all endmembers contained within our endmember library. Together with the field validation of these techniques that suggest an accuracy of ~10% (Salvatore et al., 2021), the use of a linear unmixing algorithm allows us to quickly and effectively model the presence and abundance of natural surface components over space and time with a precision and scale never before possible.

Our endmember library only consisted of actively photosynthetic microbial mats, as the reflectance of desiccated and inactive mats is not fully distinguishable from soils (Salvatore et al., 2021). Model outputs for each pixel include a percentage-of-pixel value for each endmember; the sum of all endmember percentages in a pixel = 100. RMS errors were generally highest in areas where the assumption of linear mixing is known to break down and where known surface endmembers were omitted from the spectral library. For example, the highest RMS errors throughout the scenes are always associated with snow and ice (Salvatore et al., 2020; 2021), which are spectrally distinct surface endmembers that were omitted from our endmember library (because these endmembers are not of particular interest to our investigation). To minimize the influence of these regions of high RMS error, we used a 1% RMS error threshold to indicate unacceptable model fits and to remove those pixels and model results from our dataset. A 1% RMS error threshold was used because it was sufficiently larger than typical well-modeled

portions of the landscape (RMS errors of ~0.3%) and because this thresholding also removed all pixels that are "contaminated" with snow and ice, allowing for more accurate estimates of mat coverage and abundance throughout an individual image and between images. The 1% RMS error thresholding was manually validated and determined to be adequate for the intended purposes of our investigation.

Table 1. Endmembers and bands for the image unmixing model. RMS error is not an endmember but was included as Band 6 for some images/ dates. For other images/ dates, RMS error was a separate image file rather than a band on the modeled, unmixed image.

Band #	Endmember
Band 1	Black mat
Band 2	Orange mat
Band 3	Water
Band 4	Moss
Band 5	Soil
Band 6	(RMS Error)

Processed model images were loaded into ArcGIS Pro (Version 2.7.3) for stream-scale analysis. Shapefiles corresponding to the target stream channels were created and manually adjusted to cover slightly beyond the entire stream channel width. We did this to ensure we captured the variable and anabranching flow patterns common in low-gradient MDV streams (Koch et al., 2011) over this 10-year study period. The Crescent West shapefile was divided into two separate polygons, "upper" and "lower" Crescent West, with the dividing line at the highest (farthest upstream) thermokarst border (per Sudman et al., 2017); "upper Crescent West" is above the thermokarst impacts and "lower Crescent West" is below them. This facilitates testing for within-stream biotic cover changes based on thermokarst activity. These two Crescent West polygons do not have the same area; the polygon below the thermokarst is larger. The rasterbased Zonal Statistics tool was used to assess mat coverage within these shapefiles for each stream and study year, outputting reach-wide estimates for percent cover, which we transformed to areal cover using known areal values for each shapefile and raster pixel. We use percent cover for all of our inter-reach comparisons, as the large differences in stream length and polygon size make areal outputs less intuitive to interpret. We use areal cover to report our regression analyses (regression results were similar for both metrics, and there were no shifts in significance between the two). All output data were compiled and analyzed in base R (R Core Team (2021), version 4.1.0, "Camp Pontanezen").

Benthic microbial mat data collection

We use the MCM LTER long-term microbial mat sampling record to complement and inform our biotic coverage estimates. Microbial mat samples have been collected along established transects in MDV streams since 1994, to estimate long-term biomass variation within and across the sample streams. Of our study streams, Green Creek and Von Guerard Stream have long-term transects established in 1994. Lower Crescent West has a transect that was established in 2013, in response to the thermokarst development. There is no mat sampling transect in Crescent East. For biomass assessments, the mats are commonly divided into three categories based on dominant color and community composition: orange, green and black (Alger et al., 1997; McKnight et al., 1998). Each type of mat has a different habitat preference, with black, *Nostoc*-dominated mats preferring the wetted margins of streams and orange (*Phormidium* sp. dominated) and green (*Praziolla* sp. dominated) mats preferring submersion in the middle of the channel (Alger et al., 1997; Kohler et al., 2015b; Niyogi et al., 1997; Vincent et al., 1993). Mat sampling occurs in January and has been annual since 2002; prior to 2002, these samples were collected approximately every three years. Each sampling visit collects 2-4 plugs of each type of

microbial mat that is present near each transect, using a 1.7 cm diameter brass cork borer. These samples are analyzed for AFDM by drying at 100°C for 24 hours, weighing, ashing at 450°C for 4 hours, then re-weighing to determine the mass lost to combustion (Kohler et al., 2015b).

While the biotic cover estimate and mat transect samples are very different assessments, their magnitude may still correlate, especially for chl-a. To test this, we used simple linear models between the modeled biotic cover and both AFDM and chl-a from that season's mat transect samples, using the average chl-a and AFDM values for each mat type, stream and study year. For our 'total' values, we summed the average of each mat type recorded. If there was more than one transect on a stream, we used the one closest to the stream gage site.

Streamflow

Because the presence and magnitude of streamflow is known to impact microbial mat growth and productivity (Kohler et al., 2015b), we use the MCM LTER long-term flow record to help inform our remote sensing findings. The MCM LTER has maintained a network of stream gages and water chemistry sampling sites throughout the MDVs since 1993 (currently 17 gages). These gages have in-situ sensors that yield continuous records of temperature, stage, and specific electrical conductance at 15-minute intervals during the summer flow season. Seasonallyadjusted rating curves are used to convert stage to volumetric discharge (Q, L sec⁻¹).

To illustrate streamflow for each stream over the study period, we converted each season's flow record into an exceedance probability curve (Figure 2). These curves depict the percentage of time that a stream spent at or above the streamflow value indicated on the y-axis, providing a concise summary of each flow season. However, the lowest and highest percentiles can be difficult to discern. Because these high (scouring) and zero-flow (drying) days may have

the strongest impact on microbial mat cover, we have also compiled a table summarizing these values for each stream and study year (Table 2).

To assess the influence of instantaneous flow on biomass, we use linear models comparing the stream gage record for each imagery date with the biotic cover calculated for that imagery date. We anticipate that biotic extent could be impacted by flow in two different timescales: seasonal flow would promote growth, and moderate instantaneous flow (or at least channel wetness) would promote biotic activity, which is what the sensors detect. High flows could reduce biomass by scouring (Kohler et al., 2015a). It is also possible for high flow to obscure some or all of the mat from sensor detection (M. Salvatore, personal conversation, 2022). All three of our streams are gaged. Because the gage box on Crescent stream is approximately 500 m downstream of the confluence of the east and west forks, it challenging to determine contributions to streamflow or water chemistry from each fork from gage data alone.

Water chemistry

Water chemistry samples are collected at the stream gage sites. Sample collection happens approximately weekly during the flow season for most streams. Due to intermittent streamflow and other logistics, sampling does not occur at the same time each week. Water chemistry samples are analyzed for major ions and nutrients, including NO₃ and SRP (PO₄), following the methods reported in Welch et al. (2010). All samples are filtered within 24 hours of collection and kept chilled (4°C) until analysis. Nitrile gloves are worn during sample collection to minimize organic contamination of the samples.

Thermokarst development is associated with increased nutrient loads (Bowden et al., 2008; Gooseff et al. 2016), which may stimulate growth in and below the thermokarst zone. To

assess the impact of the nutrient load on biomass, we used the Crescent Stream water chemistry nutrient data for NO₃ (the dominant N species in these streams) and PO₄ as potential drivers of increasing biomass cover. First we use Welch's t-test to test for changes in nutrient concentrations before and after 2012. We also use a linear model to test for correlations between nutrients and modeled biotic cover. Sediment loading from the thermokarst development may also be a factor impacting mat coverage (Alger et al., 1997; Bowden et al., 2008). However, MCM LTER water chemistry samples are not analyzed for total suspended solids, so we are not able to run parallel analyses that test the impact of sediment loading on mat cover.

Data availability

Mat biomass, stream gage, nutrient chemistry, and other long-term data sets are hosted at mcmlter.org and at the Environmental Data Initiative (environmentaldatainitiative.org).



Figure 2. Exceedance probability curves depict the magnitude of flow in a season. The y axis represents streamflow values for the 15-minute interval discharge record, and the y axis represents the percentage of time that the indicated discharge was equaled or exceeded. Each colored line on the plot depicts a different flow season for that stream. Streams flow approximately December-February, so for example the 2009-10 flow year corresponds with the 2010 model outputs.

Table 2. Highlighting key streamflow metrics for microbial mat areal cover. The '% time at 0' column represents days during the flow season where flow ceased or was recorded as 0. This can happen during cooler, cloudy summer periods. "NA" indicates that the data record for that period is poor or nonexistent; the amount of flow cannot be accurately determined. "PR" stands for "post record" and indicates that the season's imagery date occurred after flow recording ceased at the stream gage. It is likely that there was still liquid water in the hyporheic zone on these dates, especially higher in the reach on the two long streams (Crescent and Von Guerard).

Stream	Season	% time at 0 (no-flow periods)	Season high flow (L/s)	Seasonal flow volume (kL)	Flow season length (days)	Flow on image date (L/s)
Von Guerard	2010	17.02	465	93741	71.4	1
Von Guerard	2011	7.99	490	220504	62.1	PR
Von Guerard	2012	17.68	185	40637	55.3	1.3
Von Guerard	2013	0.06	50	16981	55.3	18.9
Von Guerard	2014	15.58	350	99655	62.0	1.5
Von Guerard	2015	37.05	95	9283	38.0	0
Von Guerard	2016	7.34	400	159144	68.0	NA
Von Guerard	2017	1.44	365	67498	65.1	17.6
Von Guerard	2018	0.00	195	NA	17.3	10.7
Von Guerard	2019	13.15	70	17495	46.0	0
Crescent	2010	20.70	60	31093	68.8	1.3
Crescent	2011	10.14	290	103823	57.3	PR
Crescent	2012	7.80	65	98712	51.6	24.3
Crescent	2013	13.20	295	38172	56.1	30.7
Crescent	2014	2.41	220	NA	57.0	19
Crescent	2015	57.24	60	24647	46.0	7.4
Crescent	2016	0.59	160	64173	76.0	NA
Crescent	2017	0.00	275	136566	53.3	8.5
Crescent	2018	11.50	40	6427	31.8	2.1
Crescent	2019	14.45	135	29058	66.2	0.5
Green	2010	5.68	210	122637	69.2	NA
Green	2011	1.62	415	304464	50.8	PR
Green	2012	8.73	285	188084	58.6	PR
Green	2013	10.34	490	267336	53.0	266.3

Green	2014	6.59	394	NA	65.0	1.6
Green	2015	7.04	240	134426	68.0	1.5
Green	2016	2.84	220	186182	79.0	NA
Green	2017	7.16	85	55236	56.4	12.6
Green	2018	29.54	65	146483	65.4	4
Green	2019	7.50	265	134426	76.5	2.2

Results

Remote sensing imagery analysis

Remote sensing analysis yielded biomass percent coverage and areal coverage (m²) estimates for all four study streams (Figure 3, Table 3, and Appendix Tables S1, S2). East Crescent had the highest coverage estimates each year. This may be due to both its length and the presence of multiple low-gradient segments of visibly high biotic activity, which persisted through most study years (Figure 4). Crescent West (whole-stream) annual mat coverage was lower than Crescent East and comparable to that of Von Guerard Stream, another long stream in this basin; and Crescent West patterns of increase and decrease roughly track those of Crescent East and Von Guerard (Figure 3), which may indicate the influence of basin-wide conditions (e.g. temperature, PAR, flow). Green Creek, which is known to host abundant microbial mats, has relatively high percent cover that varies from year to year; some of this variation may be due to the inundation of mats on the image dates (e.g. 2013 and 2017), which could render underwater mats nondetectable using our method. Inundation could occur on other streams as well; however, Green Creek has a relatively high and steady flow record during the flow season, making inundation statistically more likely.



Percent cover by year for all study streams

Figure 3. Yearly whole-stream percent cover estimates for our study reaches, 2010-2019 (2016 was omitted from analysis due to lack of clear imagery). In these stacked barplots, the height of the black segments represents black mat biomass, the height of the orange segments represents orange mat biomass, and the height of the green segments represents moss biomass.

On lower Crescent West, below the thermokarst site, percent coverage did not decline in response to the 2012 thermokarst development as expected (Figure 5). In fact, mat coverage increased in 2013, although at least part of this increase may be attributable to basin-wide variables; biomass also increased above the thermokarst site (Figure 5), and Crescent East and Von Guerard both experienced similar increases between 2012-2013 (Figure 3). The area below the thermokarst development has consistently higher biomass coverage than the area above,

which can be attributed to the larger shapefile area in the downstream segment and may also show the influence of a photosynthetically-active, small instream pond below the thermokarst site. All streams had shifting amounts of biotic cover through the study period; while there are similar trends, there were also differences by stream (Figure 3) and by the biotic type (Figure 6).

Table 3. Modeled total areal biomass cover (m^2) , summing all bands (1 (black mat) + 2 (orange mat) + 4 (moss)) for each study stream, 2010-2019. Green Creek in 2010 and all streams in 2016 were not modeled due to a lack of clear satellite imagery.

Stream	Stream length (km)	Buffered channel area (m ²)	2010	2011	2012	2013	2014	2015	2017	2018	2019
Von Guerard	4.7	9400	5602	7304	4756	6627	6571	6843	7849	7031	4991
Crescent East	5.1	10200	7965	11988	9954	15192	11286	14976	10278	7641	17901
Crescent West	4.8	9600	2623	4498	4248	6355	4111	4644	5229	2460	7258
Green	0.6	1200	NA	1188	1033	641	973	900	844	684	314



Figure 4. Representative visual image (a) and Band 1 (black mat) imagery from the lower part of Crescent Stream (both forks visible) for study years 2010 (b), 2012 (c) and 2013 (d). The red line indicates the upper end of the thermokarst activity on Crescent West. The light blue is the shapefile that was used for the model analysis. 2011 was omitted from this visualization due to lack of flow at the gage, which may make it less representative of that season's biotic cover.

White pixels indicate areas of high biotic activity or pixels that were clipped for high (> 1%) RMS error; between-year variation in RMS error is expected. Patterns of lighter pixels spread across the streambed are usually biotic, while small bands along the streambank are typically clipped snowbanks.



Figure 5. Comparing annual biomass estimates for West Crescent above (a) and below (b) the thermokarst area. The relative area of each of the sensed biota are represented in the stacked bars. 2016 was omitted from this study due to a lack of clear, cloud-free imagery that year.



Percent change in biotic areal cover by year for all study streams

Figure 6. – Percent change in biotic cover by stream and year. In the stacked barplots, green indicates change in moss cover, black indicates change in black mat cover, and orange indicates a change in orange mat cover. Bars above the 0 line indicate a positive change for that mat type from the previous year while bars below the 0 line indicate negative change from the previous year. The difference between positive and negative changes in a year = the overall change across all biota for that year.

Comparison to mat transect data

To test for correlation between transect samples and our model biotic cover estimates, we used linear regression between our estimates (for the summed area of black + orange + moss) and both transect-sampled AFDM and chl-a. Results are plotted in Figure 7. The only significant result was for Green Creek areal cover and chl-a (p = 0.04, $R^2 = 0.59$; Figure 7b).



Figure 7. Comparison of the remote sensing model biotic areal cover estimates and the transect chl-a measurements by stream. There is no mat transect on Crescent East. Only Green Creek (b.) had a significant relationship for these variables (p = 0.044, $R^2 = 0.50$).

Streamflow and biotic areal cover estimates

We tested for relationships between biotic cover and streamflow at the gage on the day each satellite image was taken. There were no significant relationships between instantaneous discharge and modeled biomass (all p > 0.05, Figure 8).

Nutrient concentrations in Crescent Stream

Comparing Crescent gage box water chemistry data before (2010-2011) and after (2013-2016) the 2012 thermokarst year, the post-thermokarst concentrations of both NO₃ and PO₄ were significantly higher than the pre-thermokarst concentrations (p = 0.045 for PO₄ and p = 0.044 for NO₃). This pulse is easiest to see in the 2013 data, especially for NO₃ (Figure 9), and it decreases over time. Neither NO₃ nor PO₄ concentrations were positively correlated with Crescent West biomass downstream of the thermokarst (both p > 0.05; Figure 10).



Figure 8. Plots comparing the modeled biotic cover to the daily average streamflow for the image collection date. There were no significant relationships (all p > 0.05).



Figure 9. NO₃ and PO₄ concentrations in Crescent Stream, 2010-2019. This plot shows nutrient concentrations by year, as measured at the Crescent Stream gage box. The y-axis was rescaled for easier visualization of the low-concentration data. Two NO₃ points are not visible with this rescaling: $NO_3 = 861.9$ in 2015, and $NO_3 = 389.0$ in 2019. In 2018, there was only one water chemistry sample, which is why that year plots as a line. Crescent Stream gage box is ~ 500 m below the confluence of Crescent East and Crescent West, and there is no formula to determine the proportion of flow or solute load from each fork at any given time.



Figure 10. Linear regressions comparing lower Crescent West's modeled areal biotic cover, below the thermokarst, on the y axis with the average nutrient load for NO₃ (a) and PO₄ (b), as measured at the streamgage, on the x axis. Regressions for the areal biotic cover and the seasonal high load for each nutrient had similar results. None of these relationships are significant (all p > 0.05); R^2 values range from -0.068 to 0.28.

Discussion

Remote sensing imagery analysis

We successfully produced the first model of annual changes to biotic cover for our four MDV stream reaches. This information can inform future studies and past interpretations with quantified data. This method is also a valuable tool that, especially in conjunction with transect biomass samples, can improve our ability to model and predict biotic changes across the valley.

Remote sensing of biocrusts and other cryptobiotic communities can be challenging because of their inherent adaptations that often shield them from direct exposure. For example, as mat communities desiccate, their photosynthetic signatures weaken and cause them to become indistinguishable from the surrounding sediments. Conversely, the spectral signatures of mat communities are weakened when they are submerged under a significant amount of water, the depth of which is dependent on properties including its opacity and turbidity. Finally, the dominant pigment composition of each community determines their dominant habitats within and surrounding the stream channels, and so the ability to detect, map, and quantify the abundance of each individual community can be complicated by localized controls on the distribution of the mat communities. For all of these reasons, remote sensing is generally considered to be an underestimate of total biotic cover in and around the Antarctic streams.

Despite these limitations, historical remote sensing data and modern studies to expand its utility provides one of the few abilities to directly observe and study past ecological processes. This study demonstrates how validated remote sensing data can be used to assess the ecological impact of a localized hydrological event in Antarctica nearly a decade in the past to demonstrate both the short- and long-term resilience of these microbial ecosystems.

Thermokarst impact on mat extent and nutrients

Contrary to expectations, our biomass model does not indicate any reduction of biotic activity in lower Crescent West after the 2012 thermokarst development. Visual reports and images from 2012 show a buried and silty channel; yet, in spite of the movement of 4.7 m³ of sediment from the banks into the channel between 2012-13 (Sudman et al., 2017), there was a 2013 increase in modeled biotic cover. This corresponds with a high (relative to Green and Von Guerard) measurement of AFDM and chl-a from the new lower Crescent West mat transect. We cannot compare pre-thermokarst mat transect measurements on Crescent West itself, as this transect was only established in 2013. The 2013 biocover increase is also seen in other streams and reaches (upper Crescent West; Crescent East; and Von Guerard), so the 2013 season likely experienced region-wide conditions that favored mat growth; however, it is notable that the thermokarst impacts did not prevent lower Crescent West from sharing this increased biotic cover.

There is also a significant increase in both NO₃ and PO₄ starting in 2013 (Figure 9), which is consistent with other studies regarding nutrient loading after a thermokarst event (Bowden et al. 2008; Gooseff et al., 2016). The impact on NO₃ levels endures for several seasons; with the exception of 2014, NO₃ levels at the Crescent gage are significantly higher than pre-thermokarst concentrations through 2019, the end of our study period. A significant result at the gage site is particularly noteworthy, as the flow at the gage box is a mix of flow from Crescent East and Crescent West forks; at any level of mixed flow, the lower concentrations from Crescent East would have a diluting effect on the thermokarst-impacted concentrations from Crescent West. This mixed-flow may explain the low NO₃ concentrations measured in 2014; these may simply indicate that the grab samples were taken when Crescent East was the dominant or only flow source at the gage.

While the 2013 increase in biotic cover is part of a basin-wide trend, the nutrient loading may have had some impact on lower Crescent West biota. In spite of visibly degraded (silted, buried) habitat, biotic cover modeled on photosynthetic activity did not decrease as expected. It is possible that the increased nutrient load from the thermokarst activity did in fact support biotic growth, and prevented a severe post-thermokarst decrease in biotic cover in the lower section of Crescent West.

Green Creek, which is known to have high microbial mat cover (Alger et al., 1997), has a much lower areal coverage than any of the other reaches. This agrees with the results of other studies (Power et al., 2020; Salvatore et al., 2021). There are several factors that may contribute to our results for Green Creek. First, it is much shorter than any of the other reaches, so has far less area to cover. Second, the analysis for Green Creek was restricted to the stream, omitting the ponded area at the top of the reach, and Green does not have mid-stream ponding; in contrast,

Crescent East and West both contained small mid-stream ponds and other areas of low, diffuse flow, which are preferred mat habitat (Alger et al., 1997, Kohler et al., 2015b). These ponds and low-flow areas are visibly-high loci of biotic activity in our spectral analysis (e.g. Figure 4) and likely increased the coverage estimates for both forks of Crescent Stream. Finally, stream gage records show that much of the Green Creek imagery was collected during periods of no flow (2011-12), low flow (2014-15, 2019) or very high flow (2013); the latter could depress activity and biotic extent, while the high flow could either scour or cover biomass with enough water to render it undetectable by remote sensing analyses.

Mat biomass

We did not find a correlation between the transect samples and our areal imagery. This is not surprising, as these are very different types of sampling. This lack of result lends strength to the suggested method of using both methods in tandem to provide an extensive and groundtruthed estimate of whole-stream mat biomass. A fruitful endeavor for the future would be to sample mats more broadly along streams near the time of the RS data collection to better identify spot/pixel correlations between the two measurement approaches.

Streamflow

We know that streamflow is a control on microbial mat biomass and growth (e.g. Kohler et al., 2015b). At various times, both lack of flow and high (scouring) flow appear to impact biomass in individual streams, which supports the findings of other MDV studies (Cullis et al., 2014; Kohler et al. 2015a, 2015b). For example, the flow-extent relationships noted for Green Creek; also the 2018 season, which had an unusually short flow season for the long streams (Crescent, Von Guerard) and low flow in all streams (Table 2). All streams have a decreased areal biomass in this year (Figure 3). However, this could also be demonstrating the influence of PAR on both streamflow and biotic activity. Ultimately, none of these results were significant (all p > 0.05), indicating that while streamflow may impact mat biomass and areal extent, there are other important co-variables that were not included in this study.

Resilience

A key takeaway from this study is the apparent resilience of MDV microbial mats to high levels of disturbance. This study indicates that they can thrive, even after being flushed with several cubic meters of sediment in a few months' time; this is a surprising result, as it has long been established that mats do not grow well in unstable or sandy habitats (Alger et al., 1997). We do know these mats are resilient in other ways; they are adapted to survive the polar desert winters and summers. McKnight et al. (2007) demonstrated that they could survive a decade of desiccation in this harsh Antarctic environment. Kohler et al. (2015a) evaluated microbial mat recovery from scour; and found that it occurs, but only over several seasons. Given this documented slow recovery from scour, it seems that either the mats did not scour at all, or that some other factor, possibly high nutrient loading from the thermokarst, ameliorated the disturbance caused by the sedimentation. This hypothesis is supported by the work of Kohler et al. (2016), who found that added nutrients stimulated growth in microbial mats. Together, these studies provide insight into various ways that microbial mats may respond under a changing Antarctic climate.

Conclusion

In spite of heavy sediment loading to the channel after January 2012, we did not find evidence of a decrease in biotic microbial mat cover in the thermokarst-impacted area of Crescent West; instead, the biotic extent increased the following year. This is a testament to the resilience of these biota.

Remote sensing analyses like this one are powerful methods for extending our sampling

"reach" and assessing stream biomass in these remote polar desert streams. This method does not

replace assessing biomass on the transects; instead the two methods complement one another.

Remote sensing analyses can only model areal cover, while transect sample plugs assess mat

density. Combining remote sensing analyses in situ, temporally-correlated transect samples can

be a useful method that provides whole-stream biomass estimates.

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Chapter V

Conclusion

As these chapters demonstrate, the ephemeral polar desert streams of the McMurdo Dry Valley [MDVs] are unique and interesting ecosystems, worthy of study both in their own right and as part of the broader LTER (and global) spectrum of stream biomes. Learning how these 'extreme streams' function is an integral part of understanding our planet as a whole; and some concepts and processes elucidated here can add to our understanding of streams in other systems. Due to their very simplicity, MDV streams can function as 'model systems' (Vitousek, 2004), elucidating broadly-applicable ecological concepts that would be more difficult to parse in more complex systems.

The study of MDV streams takes on added urgency under climate warming. As Antarctic climate change impacts continue to intensify (e.g. Chapman and Walsh, 2007; IMBIE Team, 2018; Stokes et al., 2022), MDV streams and the Dry Valleys as a whole are approaching an ecological threshold (Fountain et al., 2014; Levy et al, 2013). Increased warming in the MDVs is projected to lead to a wetter, more connected ecosystem, with greater mobility of nutrients and organic carbon (Gooseff et al., 2017; Fountain et al., 2014), as well as increased warming-related ecosystem impacts. We have already seen some of these changes. In recent years, the region has seen several precursors of a warming climate, including lake level rise, glacier ice ablation, and the thawing of lake ice and permafrost (Gooseff et al., 2017). This increase of liquid water in the system has resulted in flooding, erosion, and thermokarst subsidence (Gooseff et al., 2016, 2017; Levy et al., 2013), which in turn generate increased flows of nutrients and sediment through the streams and into the terminal lakes (Gooseff et al., 2016; Fountain et al., 2014; Levy et al., 2013). These disturbances are likely to increase; the Dry Valleys, especially the valley floors, are

in 'high risk' areas for continued warming (Fountain et al., 2014). With these streams poised on the brink of change, it becomes even more important to understand as much as we can about how MDV streams currently function, as well as to undertake research to help us assess their ecosystem response to current and future changes.

My dissertation research has focused on precisely these two areas. Chapters II and III advance understanding of under-researched aspects of MDV stream biogeochemistry and ecosystem function, including dissolved organic carbon [DOC] generation and storage and NO₃, NH₄ and PO₄ nutrient uptake dynamics across the Taylor Valley. While these topics are wellstudied in other systems, each of my chapters illuminates previously unknown dynamics for MDV streams. Then in Chapter IV, I use remote sensing to quantify the long-term stream ecosystem response to a warming-related thermokarst disturbance; my results provide new information about whole-stream biotic cover as well as the specific, disturbance response that was my focus.

In Chapter I, I leveraged the MCM LTER's long-term data record, a power law model, and an advection-reaction model to quantify patterns of dissolved organic carbon [DOC] transport and stream discharge, or the DOC-*q* relationship, in seven MDV streams. In spite of low ambient organic carbon concentrations (Aiken et al., 1996) and highly-variable streamflow (Conovitz et al., 1998), I found that the DOC-q relationship is chemostatic: it does not change across wide ranges of discharge. To explain this surprising dynamic, I developed a conceptual model of DOC generation and storage, which describes the key role the hyporheic zones play in buffering instream DOC concentrations against large changes in discharge.

In Chapter II, I modeled nutrient cycling dynamics for NO₃, NH₄, and PO₄ in six streams across the Taylor Valley, using TASCC-style pulse additions of a nutrient plus a conservative

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tracer. This was the first time that NH₄ uptake dynamics had been studied in MDV streams, as well as the first time MDV nutrient cycling dynamics have been explored on this spatial scale, across the Taylor Valley. In spite of low ambient nutrient levels, I determined that MDV uptake rates are similar to those reported in studies of temperate streams; that the hyporheic zone and hyporheic microbiota are key to nutrient cycling and transport for all three nutrients; and found clear evidence of rapid hyporheic nitrification, which supports previous work by Singley et al. (2021).

Together, these first two chapters re-emphasize the importance of hyporheic microbial communities and processes to both nutrient and carbon cycling. Benthic and hyporheic communities have interacting roles in each process (Heindel et al., 2021; McKnight et al., 2004; Singley et al., 2021; Torrens et al., 2022). Understanding the extent of these hyporheic contributions is important to a full understanding of MDV stream ecosystem ecology; and it also contributes to our understanding of temperate streams, where parallel processes likely occur but are masked by other, more easily read signals.

These chapters also provide information and insight into how the MDV, with its simple ecology and hydrology, fits into the broader spectrum of stream biomes. For example, the microbe-driven ecosystems in these ephemeral, polar desert streams are able process nutrients and carbon at rates similar to those of temperate streams (Hall et al., 2013). In multiple cases, MDV uptake rates did not saturate, indicating these biota are able to effectively utilize instream nutrients at much higher than ambient levels (> 2 orders of magnitude larger). Equally surprising is the streams' ability to maintain DOC chemostasis; in other systems, DOC chemostasis is typically seen in larger streams (e.g. 9th order and above), and is attributed to the mobilization of organic carbon stores from the riparian zone or catchment, which maintains stream DOC

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chemostasis at higher flows. This would not apply to MDV streams: they are small (first and second order) streams with no riparian zone or overland flow, and their carbon is primarily autochthonous, from microbial mats. For MDV streams, the hyporheic zone fills the role of the riparian zone in other systems, generating and storing organic carbon that buffers instream concentrations against increases in streamflow.

Finally, in Chapter IV I leveraged remote sensing imagery and analyses to assess longterm stream biotic response to a 2012 thermokarst subsidence event. This warming-related disturbance loaded 4.7 m³ of sediment from the banks into the channel between 2012-13 (Sudman et al. 2017). Sediment loading, especially at this volume, is potentially devastating for these microbial-mat dominated ecosystems; MDV mats are vulnerable to scour and burial, and do not thrive in sandy or shifting soils (Alger et al., 1997; Kohler et al. 2015b). While physical changes from the event are well-studied (Gooseff et al., 2016; Sudman et al., 2017), there were two major impediments to assessing microbial mat response to the thermokarst disturbance: 1) the lack of pre-thermokarst biomass data on the impacted reach and 2) the absence of wholestream biomass data for any MDV stream. Remote sensing imagery and a recently-developed method (Salvatore et al., 2021) allowed me to overcome these limitations and model wholestream biotic percent and areal coverage for the thermokarst-impacted reach over a 10-year span, from January 2010-January 2019. I also modeled cover for three other 'reference' streams in the basin, over the same timespan. This study increased knowledge of how whole-stream biotic cover changes over time in MDV streams, and also improved our understanding of biotic response to the 2012 disturbance. Surprisingly, biotic cover in the impacted reach actually increased in 2013, perhaps due to the large influx of nutrients (NO3 and PO4) that accompanied the sediment loading. This finding complements my nutrient uptake study (Chapter III), which

demonstrated that stream biota are capable of adjusting to large and rapid increases in nutrient loading without experiencing uptake saturation. This also implies they may be able to reduce the predicted warming-related nutrient loading to the MDV's terminal lakes.

These results are a testament to the resilience of these stream microbial communities, and indicate that at least some kinds of warming-related disturbances will not diminish MDV stream ecosystem function. They also add to our understanding of both the limits and capacities of MDV stream ecosystem resilience.

However, while heartening, this rapid ecosystem recovery is only part of the story. I studied the ecosystem-level response but not the community or population level. Climate-related changes often shift community composition; invasive species or generalist species become able to outcompete endemic species that were adapted to the previous conditions (Rahel & Olden, 2008; Vitousek et al., 1997a). There are indications that this will happen in MDV streams as well. A simulated increase in nutrients and organic matter shifted microbial communities towards generalist species and also caused an overall drop in community diversity (Buelow et al., 2016). This reinforces the importance of ongoing monitoring and research on these (and other) stream ecosystems.

Individually and as a whole, my findings have expanded our understanding of MDV stream ecosystem function, including biogeochemical cycling of nutrients and carbon and how these systems may respond to disturbance. This work also affirms the importance of long term ecological monitoring sites and programs, which provide insight into long-term processes and interactions, including ecosystem responses to a changing climate.

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Appendices:

Chapter II supplemental info:

Introduction:

Table S2.1 contains information about the study streams and their Si model parameters and Si-q curve shape factors. This table parallels Table 1 in the main text, which provides the same information for DOC.

Table S2.2 clarifies the different sampling timelines for the three major datasets used in this study: stream discharge, water chemistry (DOC and Si), and microbial mat biomass. These are reported in the main manuscript. This figure has been added to increase clarity and transparency re: these sampling timelines.

Figure S2.1 is a graph of dissolved organic carbon [DOC] vs. microbial mat ash-free dry mass [AFDM] for the four study streams that have a long-term record of microbial mat sampling. None of these relationships were significant (all p > 0.05). These results were reported in the main manuscript, but not depicted due to the lack of statistical significance. This figure supports that information.

Figure S2.2 is a graph of linear regressions for the Si-q curve shape factors vs. the median transit time (τ_f) and equilibrium time scale (τ_{eq}). All relationships for τ_f are significant (all p < 0.05), and there are no significant relationships for any of the τ_{eq} regressions (all p > 0.05). This information parallels Figure 5 in the main text, which provides the same information for DOC.

Stream	Length (m)	$q_{\rm med}$ (m day ⁻¹)	$ au_{f^{ ext{med}}}$ (day)	Ceq (mg l ⁻¹)	b	CV_c/CV_q	Damed
Aiken	2760	48.14	22.93	1.00	-0.01	0.20	39.98
Canada	700	54.93	5.10	0.73	-0.13	0.20	2.08
Crescent	5500	34.56	63.66	3.48	-0.01	0.11	25.93
Delta	7510	24.07	124.81	1.99	-0.03	0.09	38.36
Green	700	69.74	4.02	0.64	-0.10	0.27	1.62
Lost Seal	2000	75.29	10.63	1.24	-0.09	0.22	3.12
VG	4700	22.83	82.33	2.14	-0.02	0.11	41.11

Table S2.1. Stream and Stream Si Model Parameters and Shape Factors

Table S2.2. Sampling timelines for the three core datasets used in this study: stream discharge, water chemistry (DOC and Si), and microbial mat biomass. All streams used in this study are gaged.

Dataset	Sampling frequency	Sampling type
Stream discharge (gaged)	15-minute interval throughout each flow season	Pressure sensor + rating curve
Water chemistry (DOC and Si)	Approximately weekly for gaged streams	Manual grab samples
Microbial mat biomass	Annually, in January, since 2002; approximately every 3 years from 1994-2002	Manual point sampling at established transects



Figure S2.1. Relationship between mean annual dissolved organic carbon (DOC) and mean annual ash-free dry mass (AFDM) from streambed samples (all p > 0.05) in the four study streams. The plot margins show boxplots of the distributions for AFDM (top margin) and DOC (right margin) for each stream.



Figure S2.2. These scatterplots depict the values of the three Si-q shape parameters (y-axes) and either the mean transit time at median q (τ_f ; x-axes for plots a, c, e) or the equilibrium time scale (τ_{eq}); x-axes for plots b, d, f). All three relationships for τ_f are significant (all p < 0.05), and there are no significant relationships for any of the τ_{eq} regressions (all p > 0.05).

Chapter III supplemental info:

Introduction:

Figures S3.1-3.7: These Sw-nutrient curves were used to assess ambient uptake and to describe uptake behavior for each nutrient addition. Some examples were shown in the main text; all of the Sw-nutrient curves are shown below. Streams are ordered by distance from coast.



Figure S3.1: Von Guerard Stream Sw-total nutrient curves



Figure S3.2: Crescent East Fork 1516 Sw-total nutrient curves



Figure S3.3: Crescent East Fork 1617 Sw-total nutrient curves



Figure S3.4: Crescent West Fork Sw-total nutrient curves



Figure S3.5: Green Creek Sw-total nutrient curves



Figure S3.6: Priscu Stream Sw-total nutrient curves



Figure S3.7: Lawson Creek Sw-total nutrient curves

Chapter IV supplemental info:

Introduction:

The chapter text showed modeled percent biotic cover and areal (m²) biotic cover for the combined bands 1 (black mat), 2 (orange mat), and 4 (moss). <u>Table S4.1</u> shows the precise breakdown of biotic cover (% and m²) for each of the bands, for each whole stream, as well as the summed total. <u>Table S4.2</u> provides the same information for Crescent West, both above and below the upper boundary of the thermokarst impact. <u>Figures S4.1-3</u> are photographs taken at the West Crescent thermokarst site, to provide visual context.

Table S4.1: Biotic cover (both as % cover and m^2) for all study years and each of the modeled imagery bands (1 = black mat, 2 = orange mat, 4 = moss, all = 1+2+4), for the four streams in this study: Von Guerard (VG), East Crescent (CE), West Crescent (CW), and Green.

Stream	Date	Year	black_ m2	black_ perc	orange_ m2	orange_ perc	moss_m 2	moss_pe rc	all_m2	all_per c
CE	20100213	2010	5904	6.56	1350	1.5	711	0.79	7965	8.85
CE	20110209	2011	9306	10.34	1593	1.77	1089	1.21	11988	13.32
CE	20120129	2012	6093	6.77	3069	3.41	792	0.88	9954	11.06
CE	20130105	2013	6939	7.71	7407	8.23	855	0.95	15192	16.88
CE	20140201	2014	7515	8.35	2925	3.25	855	0.95	11286	12.54
CE	20150123	2015	11673	12.97	2286	2.54	1017	1.13	14976	16.64
CE	20170125	2017	4392	4.88	5220	5.8	675	0.75	10278	11.42
CE	20180119	2018	1359	1.51	5886	6.54	396	0.44	7641	8.49
CE	20190126	2019	11106	12.34	6354	7.06	441	0.49	17901	19.89
CW	20100213	2010	825.6	0.96	1410.4	1.64	387	0.45	2623	3.05
CW	20110209	2011	2433.8	2.83	1548	1.8	516	0.6	4498	5.23
CW	20120129	2012	2175.8	2.53	1582.4	1.84	490.2	0.57	4248	4.94
CW	20130105	2013	3242.2	3.77	2640.2	3.07	481.6	0.56	6355	7.39
CW	20140201	2014	2055.4	2.39	1573.8	1.83	481.6	0.56	4111	4.78
CW	20150123	2015	2459.6	2.86	1677	1.95	498.8	0.58	4644	5.4
CW	20170125	2017	2115.6	2.46	2580	3	541.8	0.63	5229	6.08
CW	20180119	2018	920.2	1.07	1264.2	1.47	275.2	0.32	2460	2.86
CW	20190126	2019	2786.4	3.24	3956	4.6	516	0.6	7258	8.44
Green	20110209	2011	810	6.75	229.2	1.91	147.6	1.23	1188	9.9
Green	20120129	2012	768	6.4	136.8	1.14	128.4	1.07	1033	8.61
Green	20130105	2013	336	2.8	243.6	2.03	60	0.5	641	5.34
Green	20140201	2014	525.6	4.38	338.4	2.82	109.2	0.91	973	8.11
Green	20150123	2015	546	4.55	282	2.35	72	0.6	900	7.5
Green	20170125	2017	487.2	4.06	302.4	2.52	54	0.45	844	7.03
Green	20180119	2018	357.6	2.98	267.6	2.23	58.8	0.49	684	5.7
Green	20190126	2019	33.6	0.28	246	2.05	34.8	0.29	314	2.62

VG	20100213	2010	2021	2.15	2547.4	2.71	1043.4	1.11	5602	5.96
VG	20110209	2011	2406.4	2.56	4239.4	4.51	658	0.7	7304	7.77
VG	20120129	2012	2603.8	2.77	1701.4	1.81	451.2	0.48	4756	5.06
VG	20130105	2013	3261.8	3.47	2650.8	2.82	705	0.75	6627	7.05
VG	20140201	2014	3064.4	3.26	2444	2.6	1052.8	1.12	6571	6.99
VG	20150123	2015	1936.4	2.06	4342.8	4.62	564	0.6	6843	7.28
VG	20170125	2017	2124.4	2.26	4718.8	5.02	1015.2	1.08	7849	8.35
VG	20180119	2018	761.4	0.81	5959.6	6.34	300.8	0.32	7031	7.48
VG	20190126	2019	2368.8	2.52	2368.8	2.52	244.4	0.26	4991	5.31

Table S4.2: Biotic cover (both as % cover and m^2) for all study years and each of the modeled imagery bands (1 = black mat, 2 = orange mat, 4 = moss), for West Crescent both above and below the 2012 thermokarst impact.

Location	Date	Voor	black_	black_	orange	orange	moss_ m2	moss_	all_m 2	all_pe
halaw	20100212	2010	609.4	1 17	2	_pere	270.4	0.52	2 1977	2 6 1
below	20100213	2010	008.4	1.17	995.2	1.91	270.4	0.52	18//	5.01
above	20100213	2010	251.6	0.74	465.8	1.37	122.4	0.36	840	2.47
total	20100213	2010	825.6	0.96	1410.4	1.64	387	0.45	2623	3.05
below	20110209	2011	1440.4	2.77	1034.8	1.99	343.2	0.66	2818	5.42
above	20110209	2011	986	2.9	540.6	1.59	183.6	0.54	1714	5.04
total	20110209	2011	2433.8	2.83	1548	1.8	516	0.6	4498	5.23
below	20120129	2012	1414.4	2.72	1092	2.1	312	0.6	2818	5.42
above	20120129	2012	792.2	2.33	533.8	1.57	183.6	0.54	1510	4.44
total	20120129	2012	2175.8	2.53	1582.4	1.84	490.2	0.57	4248	4.94
below	20130105	2013	1950	3.75	1903.2	3.66	270.4	0.52	4129	7.94
above	20130105	2013	1285.2	3.78	829.6	2.44	204	0.6	2319	6.82
total	20130105	2013	3242.2	3.77	2640.2	3.07	481.6	0.56	6355	7.39
below	20140201	2014	1196	2.3	1008.8	1.94	291.2	0.56	2496	4.8
above	20140201	2014	843.2	2.48	581.4	1.71	190.4	0.56	1618	4.76
total	20140201	2014	2055.4	2.39	1573.8	1.83	481.6	0.56	4111	4.78
below	20150123	2015	1253.2	2.41	1289.6	2.48	332.8	0.64	2876	5.53
above	20150123	2015	1132.2	3.33	476	1.4	176.8	0.52	1788	5.26
total	20150123	2015	2459.6	2.86	1677	1.95	498.8	0.58	4644	5.4
below	20170125	2017	1003.6	1.93	1762.8	3.39	296.4	0.57	3063	5.89
above	20170125	2017	1023.4	3.01	877.2	2.58	238	0.7	2139	6.29
total	20170125	2017	2115.6	2.46	2580	3	541.8	0.63	5229	6.08
below	20180119	2018	608.4	1.17	556.4	1.07	182	0.35	1347	2.59
above	20180119	2018	326.4	0.96	642.6	1.89	98.6	0.29	1068	3.14
total	20180119	2018	920.2	1.07	1264.2	1.47	275.2	0.32	2460	2.86
below	20190126	2019	1560	3.00	2990	5.75	192.4	0.37	4737	9.11

above	20190126	2019	1190	3.5	1152.6	3.39	289	0.85	2632	7.74
total	20190126	2019	2786.4	3.24	3956	4.6	516	0.6	7258	8.44

Figure S4.1-3 Select images (taken in 2015) depicting the stream channel and thermokarst subsidence on West Crescent Stream.



Figure S4.1



Figure S4.2



Figure S4.3