

PHYSICAL AND CHEMICAL CONTROLS ON THE ABUNDANCE AND COMPOSITION
OF STREAM MICROBIAL MATS FROM THE MCMURDO DRY VALLEYS,
ANTARCTICA

by

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Physical and chemical controls on the abundance and composition of stream microbial mats from the McMurdo Dry Valleys, Antarctica

Thesis directed by Professor Diane M. McKnight

ABSTRACT

The McMurdo Dry Valleys of Antarctica are a cold, dry desert, yet perennial microbial mats are abundant in the ephemeral glacial meltwater streams that flow during austral summers. Three types of mats are present (orange, black, and green), and are primarily comprised of filamentous cyanobacteria, *Nostoc*, and chlorophytes, respectively. Mat types furthermore occupy distinct habitats within streams, utilizing the benthos, hyporheic zone, and water column, which expose them to different environmental conditions. Due to a lack of lateral inflows, allochthonous organic inputs, and negligible grazing activity, these streams are ideal for the controlled ecological study of microbial mats. Here, I investigated how mats will respond to physical disturbance, alterations in the hydrologic regime, and nutrient liberation from permafrost melt in the future. Specifically, I: 1) quantified and characterized the regrowth of mat biomass, community structure, and elemental stoichiometry after a scouring disturbance, 2) investigated how geomorphology and taxonomic identity influences the response of mat biomass to hydrologic regime in transects monitored over two decades, and 3) evaluated relationships between water chemistry and the elemental and isotopic composition of mat types over longitudinal and valley-wide gradients in Taylor Valley. I found that mats recovered ~20-50% of their biomass over the course of an austral summer following scour. Algal communities were significantly different in composition between disturbed and control treatments, but all samples naturally varied in species and elemental stoichiometry over the study period. When the long-term record of mat biomass was compared with hydrologic variables, stream channel mats (orange and green) had the greatest correlations, while marginal mats (black) showed weaker relationships with flow regime. Relationships also differed as a function of stream geomorphology, indicating the importance of substrata and gradient in conjunction with discharge. Lastly, mats showed unique elemental and isotopic compositions. Green and orange mats within the stream channel most reflected water column nutrient concentrations, while black mats showed significant nitrogen fixation. These results highlight the importance of taxonomic identity and habitat to modeling primary production here and elsewhere, and provide insight to how stream microbial mat communities are formed, maintained, and ultimately persist in an isolated polar desert.

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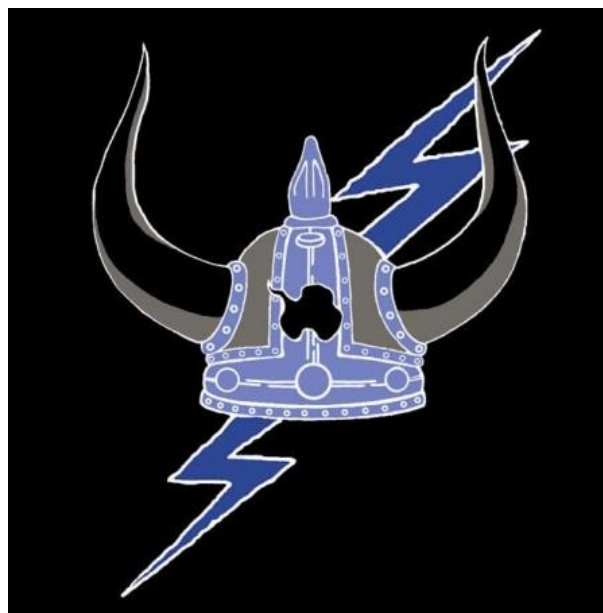
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-Tabasco Kid



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CHAPTER I

ANTARCTIC STREAM ECOLOGY

“In this valley and in this lake and in the sediments beneath, these cycles turned in miniature, in a space that was comprehensible, but that was tied nonetheless into the larger space of the world.”
-Bill Green, from *Water, Ice, and Stone*

INTRODUCTION

The McMurdo Dry Valleys (MDVs, 76830'–78800'S, 160800'–165800'E) represent the < 2% of Antarctica that is ice-free, and are generally considered one of Earth's coldest, driest deserts (McKnight et al. 1999, Figure 1). Despite the relatively barren terrain, the MDVs contain an extensive network of streams that are activated during summer glacial melt, and drain into perennially frozen lakes on the valley floor (Fountain et al. 1999, McKnight et al. 1999). Unlike most other stream systems, MDV streams have no riparian vegetation, terrestrial inputs, only negligible grazing activity, and are fed solely by glacial meltwater (Treonis et al. 1999, Gooseff et al. 2011). Therefore, environmental heterogeneity produced by grazers (ex. McIntyre et al. 2008), variation in canopy cover (ex. Bixby et al. 2009), or anthropogenic activity in watersheds (ex. Kemp and Dodds 2001) is almost completely absent. These conditions make the MDVs an ideal place to study fundamental mechanisms regulating primary producers.

Because of this relative simplicity, the MDVs have been designated as an end member for the United States Long-Term Ecological Research (LTER) program. Investigations into the MDV streams were initiated by the New Zealand Antarctic Program in the late 1960's and included discharge measurements of the Onyx River in Wright Valley in 1971 (Chinn 1993). Stream gaging stations in the adjacent Taylor Valley have been operated by the MCMLTER in collaboration with the U.S. Geological Survey since the early 1990's (mcmlter.org). Microbial

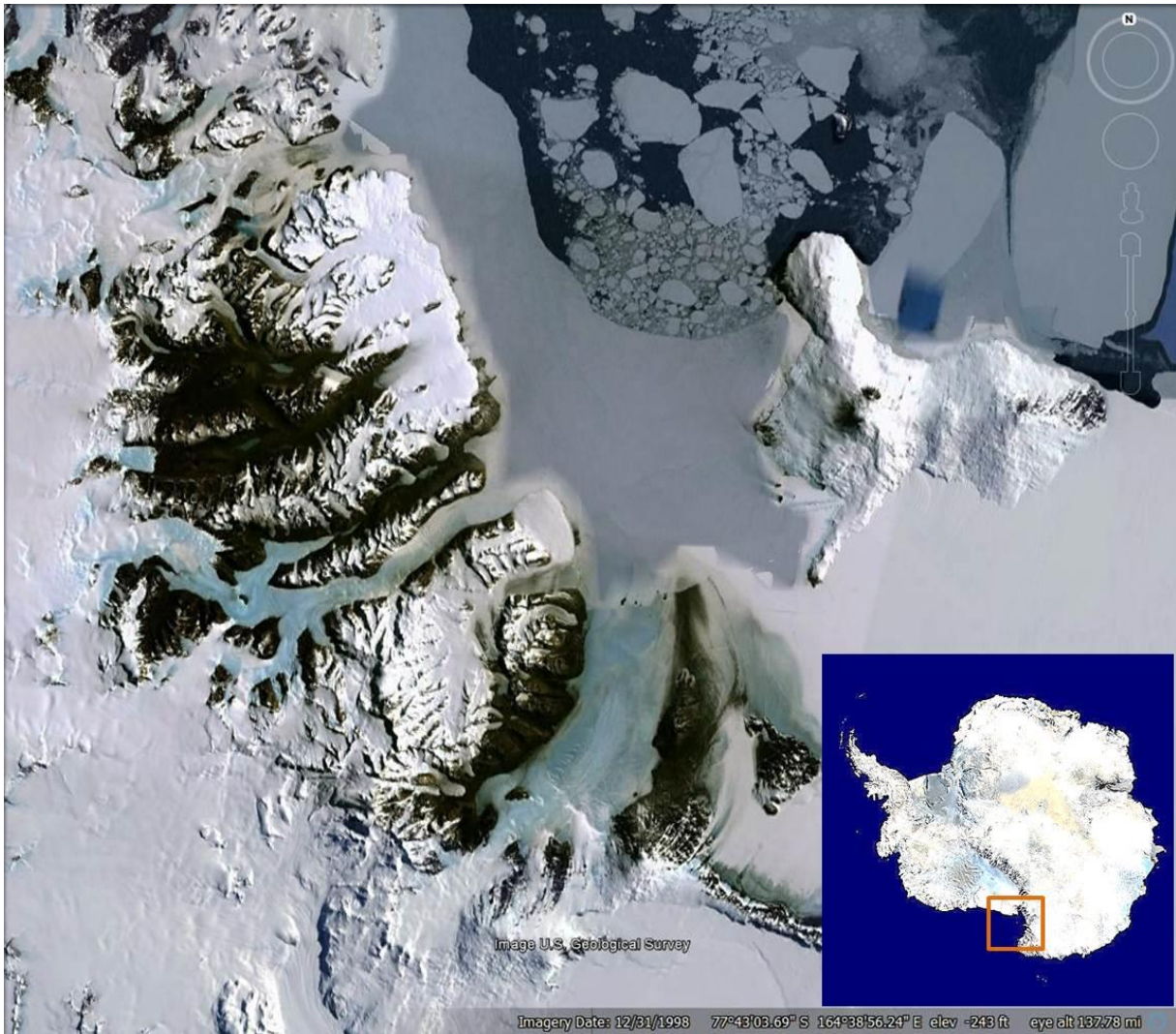


Figure 1. Map of Antarctica, Ross Island, and the McMurdo Dry Valleys. Map data ©2015 Google.

mats are widespread throughout MDV streams, with *Nostoc* and green algae communities present in lesser abundances. These communities not only differ from one another in their taxonomic composition and appearance (Alger et al. 1997, Vincent and Quesada 2012), but also in their in-stream habitat preference which exposes mats to different physical conditions throughout summer months. Sixteen diverse stream algal transects have been monitored since the 1993-94 summer by the MCMLTER (Figure 2, Table 1), and four different microbial community types (all referred to as “mats” for brevity) have been historically monitored (Figure 3).

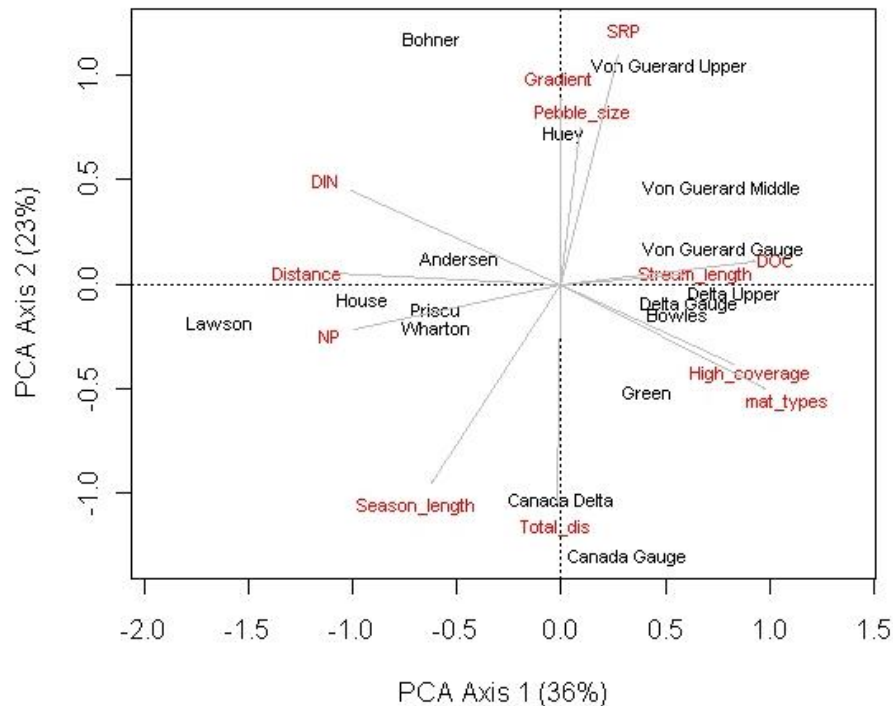


Figure 2. PCA showing the physical diversity of the 16 original stream transects monitored in Taylor Valley by the MCMLTER.

Table 1. Sample history for MCMLTER transects over the last 20 years. Transects are in approximate order from west to east. “Yes” indicates samples were taken from a transect in a given season, and “NS” means the transect was not sampled. “No mats”, “few mats”, “no flow”, “lost”, and “little flow” indicate a transect was visited but was not sampled or data are not available for that given reason. Abbreviations for stream transects are given in Table 1 of Chapter III.

	LAW	PRC	BOH	WHR	HOU	AND	CAN-G	CAN-D	BOW	GRN	DLT-G	DLT-U	HUE	VNG-G	VNG-M	VNG-U
93-94	Yes	Yes	Yes	Yes	no mats	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
94-95	NS	Yes	Yes	Yes	no mats	NS	Yes	Yes	NS	Yes	NS	NS	NS	NS	Yes	NS
95-96	NS	NS	NS	NS	NS	NS	Yes	NS	NS	NS	NS	NS	NS	NS	Yes	NS
96-97	NS	NS	NS	NS	no mats	no mats	NS	NS	Yes	Yes	NS	NS	NS	Yes	Yes	Yes
97-98	NS	NS	NS	NS	NS	NS	lost	lost	lost	lost	lost	NS	NS	lost	NS	NS
98-99	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
99-00	NS	NS	NS	NS	NS	NS	NS	NS	NS	Yes	little flow	NS	NS	No flow	NS	NS
00-01	no mats	no mats	Yes	Yes	NS	no mats	Yes	NS	Yes	Yes	Yes	Yes	Yes	No flow	few mats	Yes
01-02	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
02-03	no mats	Yes	NS	Yes	Yes	no mats	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
03-04	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
04-05	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
05-06	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
06-07	Yes	no mats	Yes	Yes	Yes	no mats	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
07-08	NS	NS	NS	Yes	NS	NS	Yes	NS	Yes	Yes	Yes	NS	NS	Yes	NS	Yes
08-09	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
09-10	Yes	Yes	NS	NS	NS	NS	Yes	NS	Yes	Yes	Yes	NS	NS	Yes	Yes	NS
10-11	NS	NS	Yes	NS	NS	NS	Yes	NS	Yes	Yes	Yes	Yes	NS	Yes	NS	NS
11-12	no mats	Yes	Yes	Yes	Yes	no mats	Yes	NS	Yes	Yes	Yes	NS	NS	Yes	Yes	NS
12-13	Yes	Yes	Yes	Yes	NS	no mats	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes

MDV microbial communities

Microbial mats are layered, coherent structures formed by a diverse assemblage of entangled organisms that live together and exchange materials to enhance their component parts (Paerl et al. 2000, Stal 2000). Preserved stromatolites are hypothesized to be the first evidence of these communities, which may have been similar to structures found in Mexico (Elser et al. 2006), Australia (Papineau et al. 2005), and Antarctica (Andersen et al. 2011). During the early history of the earth, mats likely contributed to the oxygenation of our atmosphere (Hoehler et al. 2001, Schirrmeister et al. 2013), aided in the formation of Precambrian soils (Dodds et al. 1995), and were likely dominant ecological players during widespread glaciations (Vincent et al. 2000, Vincent and Howard Williams 2000, Vincent et al. 2004). However, with the rise of metazoans, mats became restricted to areas of low grazing pressure, including chemically and thermally stressed environments, arid deserts, and polar freshwaters (Paerl et al. 2000, Vincent 2000, Vincent and Quesada 2012).

Microbial mats are capable of surviving long periods frozen and dried (Dodds et al. 1995, McKnight et al. 2007), and possess an ability to maintain a favorable internal microhabitat regardless of external conditions (Vincent and Quesada 2012). Some mats furthermore incorporate sediment in their structure or precipitate calcite, which creates habitat, promotes stability, and may ultimately result in fossilization (Stal 2000). These characteristics make mats an excellent example of an “ecosystem engineer” (Jones et al. 1994). Nutrient concentrations may be orders of magnitude higher within the mat than in the water column above (Vincent et al. 1993a, Villeneuve et al. 2001, Mueller and Vincent 2006), and vertical mat stratification results in greatest concentrations of oxygen and pigment at upper mat layers (Bonilla et al. 2005, Lionard et al. 2012), while chlorophyll concentrations are greater below (Vincent et al. 1993b).

This organization protects sensitive lower layers from incoming UV radiation (Tanabe et al. 2010), and in some cases may allow anoxic metabolic pathways to occur (Stal 2000).

For ease of identification, microbial communities living within the MDVs are described by color, and represent coarse categories which presumably reflect taxonomic and functional distinctions. Orange and red mats are comprised of filamentous cyanobacteria such as *Oscillatoria*, *Leptolyngbya*, and *Microcoleus spp*, and are more abundant in the thalweg where flow is constant (Alger et al. 1997, Niyogi et al. 1997). While red mats are similar in composition, they are far more sparsely distributed, and appear as rubbery “tufts” (Alger et al. 1997, Niyogi et al. 1997). Black mats are formed by *Nostoc*, externally dark in color (yet sometimes bright green on the underside), and are found in abundance at stream margins where substrata are wetted but not submerged. Lastly, chlorophytes are present as small patches or streamers attached to sides or bottoms of rocks, and called “green mats” for the sake of consistency. The only eukaryotic “mat” type, these communities are often dominated by *Prasiola spp*. Any combination of mat types may be in a given stream, and when present differ in streambed coverage (Figure 4). However, what regulates the abundance of mats is poorly understood, though vital to understanding their ecologies and interpreting long-term data.

Diatoms reside within the phycosphere of all mats at low densities. Diatoms are single-celled eukaryotic algae (Bacillariaceae) with cell walls comprised of biogenic silica (Figure 5). Because of these glass “frustules”, diatoms not only preserve well in sediment, but are also relatively easy to identify (compared to chlorophytes and cyanobacteria) due to siliceous features on their exterior characteristic of a given species. Furthermore, individual diatom taxa have threshold tolerances to environmental variables, making them ideal bioindicators for monitoring

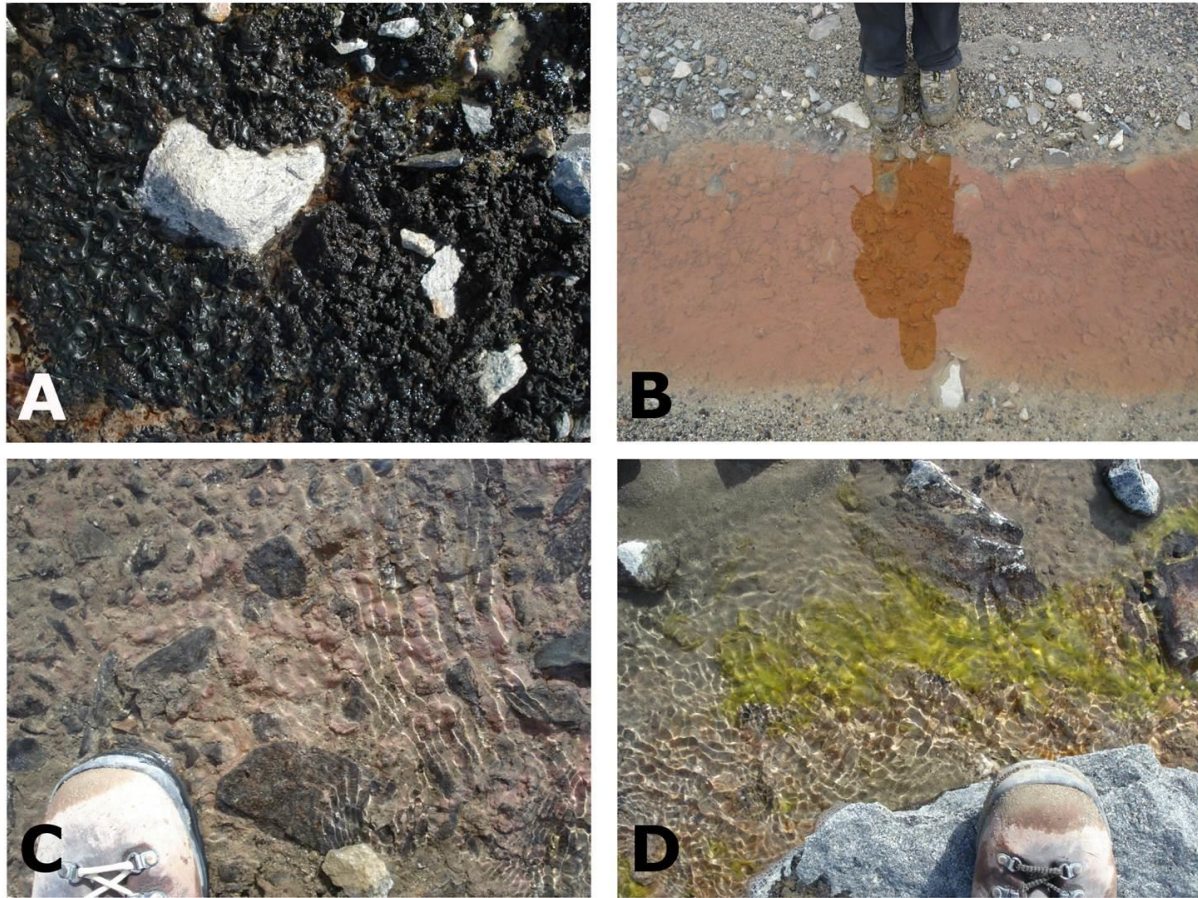


Figure 3. Photographs of the four mat types sampled in this long-term research: A) black, B) orange, C) red, and D) green.

water quality across a diversity of habitats, including the MDVs (Spaulding et al. 2010). Antarctic diatoms have previously been used to make inferences on past (Spaulding et al. 1997, Whittaker et al. 2008, Konfirst et al. 2011, Warnock and Doran 2013) and present (Roberts and McMinn 1996, Esposito et al. 2006, Stanish et al. 2011, Stanish et al. 2012, Pla-Rabes et al. 2013) environmental conditions, and other applications may eventually be possible, such as using diatoms to predict the stage of colonization, recovery, and stream nutrient status.

Research in MDV streams

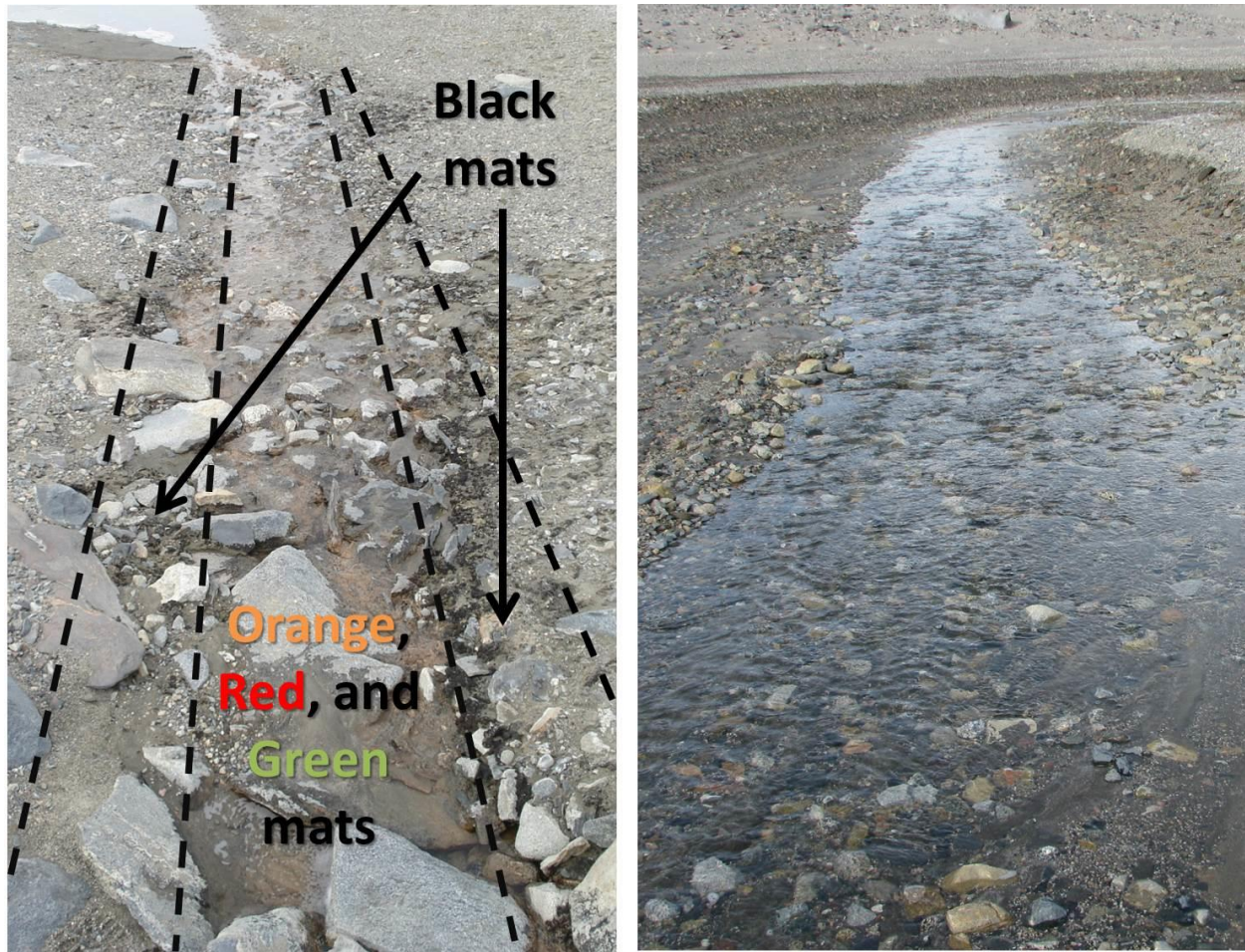


Figure 4. On left, a photo of Bowles Creek, a high coverage transect, showing the restricted marginal distribution of black mats within the streambed. On right is Priscu Stream, a low coverage transect, for comparison.

Dry Valley streams are hydrologic and biogeochemical links between glaciers and the closed basin lakes, readily intercepting, assimilating, and transforming dissolved nutrients *en route* (Gooseff et al. 2004). This may have a profound effect on the amount and type of elements reaching lakes, and outlets generally have lower nutrient concentrations than headwaters, especially when mat biomass is high (McKnight et al. 2004). However, mechanisms responsible for regulating the biomass of different MDV mat types are not well understood, though three decades of prior research has provided speculation (Vincent and Howard-Williams 1986, Howard-Williams et al. 1989, McKnight et al. 1999, Stanish et al. 2011). Furthermore, while

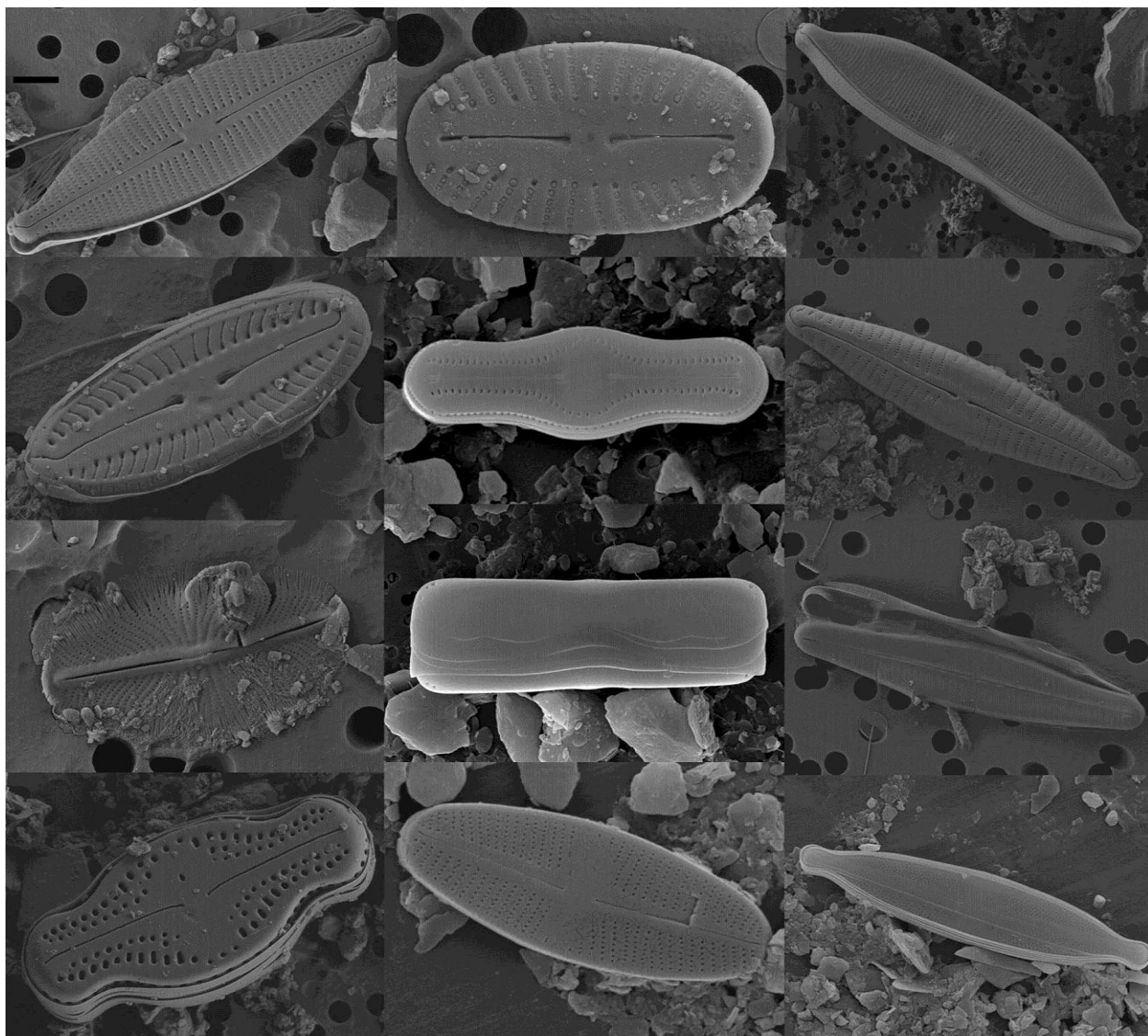


Figure 5. Scanning electron microscope images of some representative diatom taxa from the McMurdo Dry Valleys. Images courtesy of Kateřina Kopalová, Myriam de Haan, and Bart Van de Vijver.

mats are organic hotspots in an otherwise nutrient poor environment (Barrett et al. 2006), nutrient cycling by microbial mats is not well understood (Stal 2000), and the fate of assimilated nutrients within mats remains poorly documented. Thus, disentangling factors controlling uptake and storage will be necessary to understanding connectivity between MDV habitats.

In addition to modern ecology, mats have furthermore been used as an analogue to study places inaccessible through space and time, such as other planets (Elser 2003, Hage et al. 2007), Martian sediments (Doran et al. 1998, Bishop et al. 2001), and the ancient Earth (Vincent et al. 2000, Vincent and Howard Williams 2000). The stoichiometric relationships between mat communities and their environment specifically may have intriguing implications. For example, shifts in mat phosphorus content have been hypothesized to make hard body parts in grazing invertebrates possible, leading to the Cambrian Explosion (Elser et al 2006). Similarly, nitrogen-limited microbial mats may increase mucilage production, preventing calcification and in turn impacting stromatolite community ecology, evolution, and fossilization (Stal 2000). As a result, knowledge gained through the study of these communities may have far reaching applications.

While there is much to learn about MDV microbial mats, a changing climate promises to complicate their investigation. Lake levels in the MDVs have been rising since the early 20th century (Bomblies et al. 2001), although this trend was slowed by a cool period in the 1990's (Doran et al. 2002). Carbon dioxide emissions are thought to have altered the Southern Annular Mode, with the result of Southern Ocean winds south to Antarctica preventing warming in parts of East Antarctica (Abram et al. 2014). The ozone hole that has seasonally developed over the continent from past CFC use may also play a part, and with its amelioration the MDVs are expected to warm (Chapman and Walsh 2007, Walsh 2009). Regardless of cause, the cooling trend was interrupted in the summer of 2001-02 by a “flood year” (Doran et al. 2008), and lake levels have since continued to rise (Figure 6), necessitating the upward migration of camps, stream gages, and tents to higher ground (Crisp and Kohler, personal observations).

In addition to these indirect human effects, upwards of 30,000 tourists and 7,000 scientists now visit the continent each year (Chown et al. 2012), making non-native species

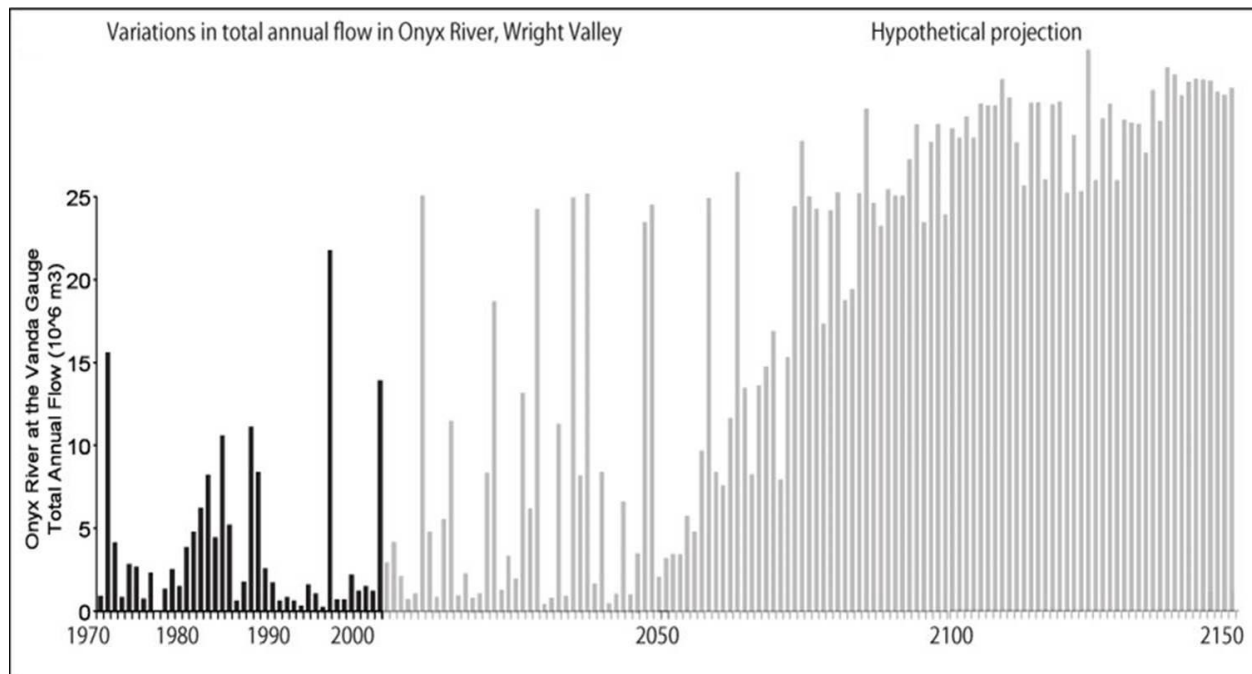


Figure 6. Total annual discharges for the Onyx River, with dark bars representing measured values and light bars representing projected values.

introductions (Huiskes et al. 2014) and the trampling of fragile desert pavement and microbial mats an increasing concern (reviewed by Tin et al. 2009). Previous studies have addressed the vulnerability of soil invertebrate communities (Ayres *et al.* 2008), moss beds and lichens (Perterra *et al.* 2013), and desert pavement surfaces (Campbell et al. 1998, O'Neill et al. 2013) to trampling, though the magnitude of this type of disturbance is not yet known for the MDV streams. Therefore, addressing the possibility of anthropogenic disturbances on microbial mats will be important for promoting regional conservation. Microbial mats from polar habitats have previously been shown to exhibit slow growth rates (Vincent and Howard-Williams 1986, Hawes et al. 2013), and while they may be tolerant to environmental changes such as increases in salinity (Bonilla et al. 2005), they are responsive to changes in radiation, temperature (Bonilla et al. 2009), and elevated discharges (Stanish et al. 2011).

The Antarctic Environmental (or Madrid) Protocol is a part of the Antarctic Treaty implemented to protect and maintain biodiversity below 60 degrees latitude. One means of preventing disturbances to sensitive areas is through implementing Antarctic Specially Protected Areas (ASPAs – e.g. Canada Stream) and Antarctic Specially Managed Areas (ASMAs – e.g. MDV region), which have special regulations and recommendations for entry. Many MDV camp sites are near streams, and ecological information is needed for these habitats to inform planners creating, maintaining, and updating facility zones. The MDVs also contain public areas accessible to tourists, and the Taylor Valley Visitor Zone which is located on the headwaters of Green Creek is a popular attraction for cruise ship passengers (O'Neill et al. 2013). Just as “recognizing and mitigating human effects” was recently listed as one of six priorities for future Antarctic research (Kennicutt et al. 2014), there is a timely need to document the intra- and inter-seasonal dynamics of microbial mats to assess their risks from anthropogenic activity.

At present, the available literature is limited by both temporal and spatial scales, hampering our ability to discern long-term microbial mat dynamics and responses to environmental changes. For example, microbial photosynthesis can be observed on a scale of minutes in response to changes in illumination, while taxonomic shifts may occur over centuries or millennia with changes in climate (Quesada et al. 2008, Figure 7). Due to the limited historical presence of humans in Antarctica, the complicated logistics of working there, and the short-term nature of grant funding cycles, most of our knowledge of MDV microbial mat ecology has been performed over the last 30 years in short-term experiments of photosynthesis (Vincent et al. 1993a), structure (Vincent et al. 1993b), and physiology (Howard-Williams et al. 1989), and generally very limited in spatial scope. While some recent literature reports observations spanning several decades, these studies are either performed in habitats such as ice shelf ponds

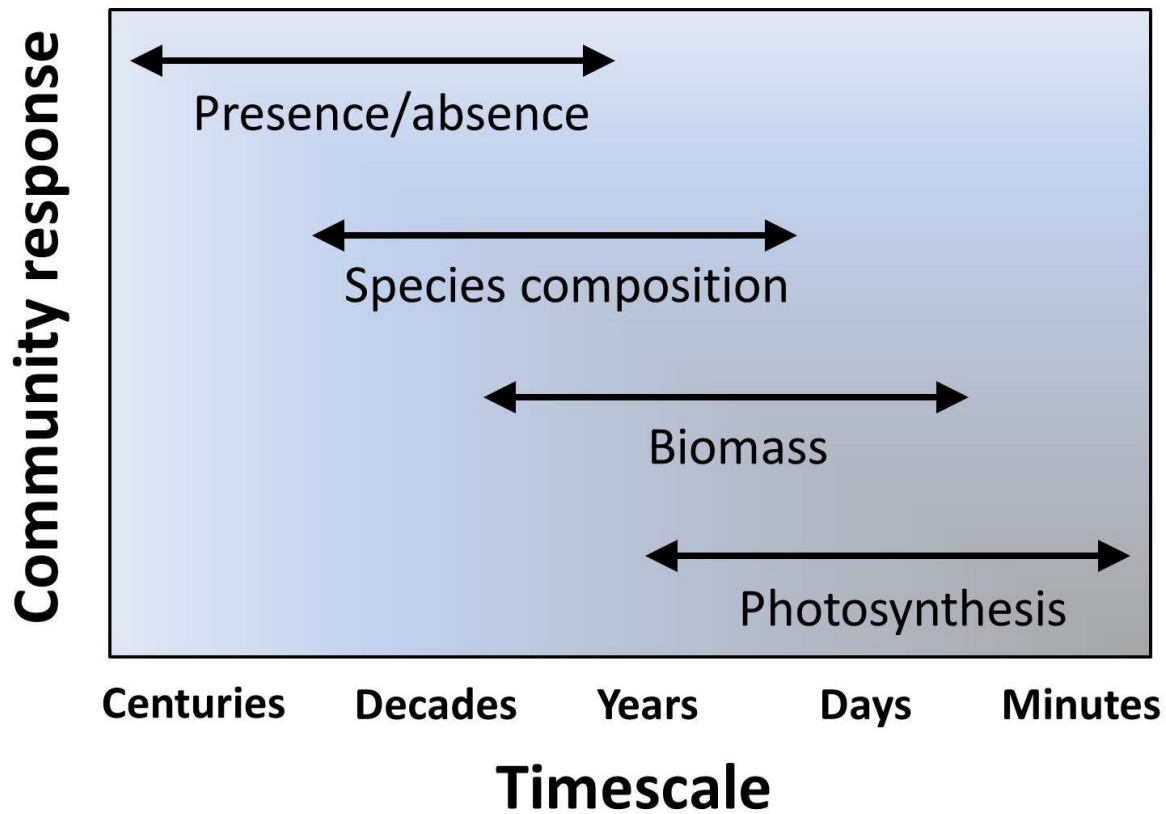


Figure 7. Conceptual diagram showing community responses to a changing environment over time. Adapted from Quesada et al. 2008.

(Hawes et al. 2014), or concentrate on specific community members such as diatoms (ex. Esposito et al. 2006, Stanish et al. 2011). Therefore, it is intensive long-term analyses over large spatial scales that is particularly lacking in the literature for Antarctic stream systems, and is a frontier for future study (Quesada et al. 2008). These shortcomings establish the impetus for this dissertation.

ARRANGEMENT OF DISSERTATION

In order to understand the ecologies of different microbial mat types, as well as project how they might respond to future direct and indirect anthropogenic pressures, I explore the effects of anthropogenic disturbance, changing hydrologic regime, and nutrient availability on microbial

mats in three chapters. Insights gained from this dissertation, along with suggestions for future research, are summarized in Chapter V. Lastly, a revision of the diatom genus *Luticola* from the McMurdo Sound Region is presented as an Appendix. These sections are outlined below in further detail:

Chapter II: Recovery of Antarctic stream epilithon from simulated scouring events. As the number of scientists and tourists visiting Antarctica increases annually, it is necessary to understand the role of disturbance in structuring microbial communities. Additionally, while it is widely assumed that scour is responsible for the reduction of biomass and changes in community structure, there are no studies at present which monitor the recovery of mats from disturbance in Antarctic streams. Here, the recovery of microbial mats from an anthropogenic disturbance is investigated by measuring biomass, elemental composition, and algal community composition on natural rock substrata over the course of a summer. These results help understand the role disturbance plays in transforming communities, which is vital for interpreting long-term data and protecting areas such as the MDVs, which fall within an Antarctic Specially Managed Area (ASMA).

Chapter III: Life in the main channel: long-term hydrologic control of microbial mat abundance in McMurdo Dry Valley streams, Antarctica. In light of results gained in the previous chapter, the long-term trends in biomass of three different stream microbial communities, which differ in their dominant taxonomic constituents and use of stream habitat, are compared with trends in different hydrologic indices incorporating discharge, floods, and droughts to test how mats respond to hydrologic variability. Streams were additionally analyzed separately as high and low

biomass transects to elucidate the role of geomorphology in regulating biomass. As the climate of the MDVs changes, we might expect overall increases in microbial mat biomass with general warming of the region. However, responses will ultimately depend on the physical characteristics of streams, the response of the dominate taxa, and the nature of multiple hydrologic indices.

Chapter IV: Isotopic and elemental composition of Antarctic stream microbial communities. The topography of the MDVs are changing, and slumping and erosion of streambanks from thermokarst development is present at several streams which may liberate nutrients. In this chapter, we first investigate how different microbial mat types vary in their biomass, elemental, and isotopic composition, and then investigate how variation within each of these variables can be explained by the nutrient concentrations both within and among streams. This study was conducted in Taylor Valley, which is situated over a geologic chronosequence and alternates in nitrogen and phosphorus availability. These results help us understand the fate of nutrients after they have been removed from the water column and assimilated, and will ultimately aid in calculating the mass balance of important elements within this changing biome.

*Appendix: The genus *Luticola* D.G.Mann (Bacillariophyta) from the McMurdo Sound Region, Antarctica, with the description of four new species.* Diatom taxonomy is a rapidly evolving discipline, and as the sub- and Maritime Antarctic floras have been recently revised using a morphological approach, a similar revision for the Antarctic continent is wanting. Particularly problematic is the genus *Luticola*, which has the greatest diversity in the McMurdo Sound Region, as well as the most taxonomic species drift. To address this, new material was collected from Ross Island (a major type locality), cryoconite holes, small ponds, and MDV streams as

part of the MCMLTER. In this appendix, we describe four new species, make one new combination, update all taxonomic designations, and extend the geographic distribution and ecology of observed *Luticola* species.

REFERENCES

- Abram, N. J., Mulvaney, R., Vimeux, F., Phipps, S.J., Turner, J., and England, M.H. 2014. Evolution of the Southern Annular Mode during the past millennium. *Nature Climate Change* 4: 564–569. doi:10.1038/nclimate2235
- Alger, A.S., McKnight D.M., Spaulding S.A., Tate, C.M., Shupe, G.H., Welch, K.A., Edwards, R., Andrews, E.D., and House, H.R. 1997. Ecological processes in a cold desert ecosystem: the abundance and species distribution of algal mats in glacial meltwater streams in Taylor Valley, Antarctica. Institute of Arctic and Alpine Research Occasional Paper 51.
- Ayres, E., Nkem, J.N., Wall, D.H., Adams, B.J., Barrett, J.E., Broos, E.J., Parsons, A.N., Powers, L.E., Simmons, B.L., and Virginia, R.A. 2008. Effects on human trampling on populations of soil fauna in the McMurdo Dry Valleys, Antarctica. *Conservation Biology* 22: 1544-1551.
- Andersen, D.T., Sumner, D.Y., Hawes, I., Webster-Brown, J., and McKay, C.P.. 2011. Discovery of large conical stromatolites in Lake Untersee, Antarctica. *Geobiology* 9:280-293. doi: 10.1111/j.1472-4669.2011.00279.x
- Barrett, J.E., Virginia, R.A., Hopkins, D.W., Aislabie, J., Bargagli, R., Bockheim, J.G, Campbell, I.B., Lyons, W.B., Moorhead, D.L., Nkem, J.N., Sletten, R.S., Steltzer, H., Wall, D.H., and Wallenstein, M.D. 2006. Terrestrial ecosystem processes of Victoria Land, Antarctica. *Soil Biology and Biogeochemistry* 38: 3019-3034. doi: 10.1016/j.soilbio.2006.04.041
- Bishop, J.L., Lougear, A., Newton, J., Doran, P.T., Froeschl, H., Trautwein, A.X., Korner, W. and Koeberl, C. 2001. Mineralogical and geochemical analyses of Antarctic lake sediments: A study of reflectance and Mössbauer spectroscopy and C, N, and S isotopes with applications for remote sensing on Mars. *Geochimica et Cosmochimica Acta* 65: 2875–2897.
- Bixby, R.J., Benstead, J.P., Douglas, M.M., and Pringle, C.M. 2009. Relationships of stream algae community structure to catchment deforestation in eastern Madagascar. *Journal of the North American Benthological Society* 28: 466-479.
- Bomblies, A., McKnight, D.M., and Andrews, E.D. 2001. Retrospective simulation of lake-level rise in Lake Bonney Based on recent 21-yr record: indication of recent climate change in the McMurdo Dry Valleys, Antarctica. *Journal of Paleolimnology* 25: 477-492.

- Bonilla, S., Rautio, M., and Vincent, W.F. 2009. Phytoplankton and phytobenthos pigment strategies: implications for algal survival in the changing arctic. *Polar Biology* 32: 1293-1303.
- Bonilla, S., Villeneuve, V., and Vincent, W.F. 2005. Benthic and planktonic algal communities in a high arctic lake: pigment structure and contrasting responses to nutrient enrichment. *Journal of Phycology* 41: 1120-1130. doi: 10.1111/j.1529-8817.2005.00154.x
- Campbell, I.B., Claridge, G.G.C. and Balks, M.R. 1998. Short and long-term impacts of human disturbance on snow-free surfaces in Antarctica. *Polar Record* 34: 15-24.
- Chapman, W.L., and Walsh, J.E. 2007. A synthesis of Antarctic temperatures. *Journal of Climate* 20: 4096-4117.
- Chinn, T.J. 1993. Physical hydrology of the Dry Valley lakes. In Green, W.J. and Friedmann, E.I., Eds. *Physical and Biogeochemical Processes in Antarctic Lakes*. Antarctic Research Series, Washington, D.C.: American Geophysical Union, 1-52.
- Chown, S.L., Huiskes, A.H.L., Gremmen, N.J.M., Lee, J.E., Terauds, A., Crosbie, K., Frenot, Y., Hughes, K.A., Imura, S., Kiefer, K., Lebouvier, M., Raymond, B., Tsujimoto, M., Ware, C., Van de Vijver, B., and Bergstrom, D.M. 2012. Continent-wide risk assessment for the establishment of nonindigenous species in Antarctica. *Proceedings of the National Academy of Science* 109(13): 4938-4943.
- Dodds, W.K., Gudder, D.A., and Mollenhauer, D. 1995. The ecology of *Nostoc*. *Journal of Phycology* 31(1): 2-18. doi: 10.1111/j.0022-3646.1995.00002.x
- Doran, P.T., Priscu, J.C., Lyons, W.B., Walsh, J.E., Fountain, A.G., McKnight, D.M., Moorhead, D.L., Virginia, R.A., Wall, D.H., Clow, G.D., Fritsen, C.H., McKay, C.H., and Parsons, A.N. 2002. Antarctic climate cooling and terrestrial ecosystem response. *Nature* 415: 517-520.
- Doran, P.T., McKay, C.P., Fountain, A.G., Nylen, T., McKnight, D.M., Jaros, C., and Barrett, J.E. 2008. Hydrologic response to extreme warm and cold summers in the McMurdo Dry Valleys, East Antarctica. *Antarctic Science* 20(5): 499-509. doi: 10.1017/S0954102008001272
- Doran, P.T., Wharton Jr., R.A., Des Marais, D.J., and McKay, C.P. 1998. Antarctic paleolake sediments and the search for extinct life on Mars. *Journal of Geophysical Research* 103: 28481-28493. doi:10.1029/98JE01713
- Elser, J.J. 2003. Biological stoichiometry: a theoretical framework connecting ecosystem ecology, evolution, and biochemistry for application in astrobiology. *International Journal of Astrobiology* 2(3): 185-193. doi: 10.1017/S1473550403001563
- Elser, J.J., Watts, J., Schampel, J.H., and Farmer, J. 2006. Early Cambrian food webs on a trophic knife-edge? A hypothesis and preliminary data from a modern stromatolite-based

- ecosystem. *Ecology Letters* 9: 295-303. doi: 10.1111/j.1461-0248.2005.00873.x
- Esposito, R.M.M., Horn, S.L., McKnight, D.M., Cox, M.J., Grant, M.C., Spaulding, S.A., Doran, P.T., and Cozzetto, K.D. 2006. Antarctic climate cooling and response of diatoms in glacial meltwater streams. *Geophysical Research Letters* 33(7): L07406.1-L07406.4. doi: 10.1029/2006GL025903.
- Fountain, A.G., Lyons, W.B., Burkins, M.B., Dana, G.L., Doran, P.T., Lewis, K.J., McKnight, D.M., Moorhead, D.L., Parsons, A.N., Priscu, J.C., Wall, D.H., Wharton, R.A., and Virginia, R.A. 1999. Physical controls on the Taylor Valley ecosystem, Antarctica. *Bioscience* 49(12): 961-971.
- Gooseff, M.N., McKnight, D.M., Doran, P., Fountain, A.G., and Lyons, W.B. 2011. Hydrological connectivity of the landscape of the McMurdo Dry Valleys, Antarctica. *Geography Compass* 5/9: 666-681. doi: 10.1111/j.1749-8198.2011.00445.x
- Gooseff, M.N., McKnight, D.M., Runkel, R.L., and Duff, J.H. 2004. Denitrification and hydrologic transient storage in a glacial meltwater stream, McMurdo Dry Valleys, Antarctica. *Limnology and Oceanography* 49(5): 1884-1895.
- Hage, M.M., Uhle, M.E., and Macko, S. 2007. Biomarker and stable isotope characterization of coastal pond-derived organic matter, McMurdo Dry Valleys, Antarctica. *Astrobiology* 7(4): 645-661. doi: 10.1089/ast.2006.0033
- Hawes, I., Howard-Williams, C., and Sorrell, B. 2014. Decadal timescale variability in ecosystem properties in the ponds of the McMurdo Ice Shelf, southern Victoria Land, Antarctica. *Antarctic Science* 26(3): 219-230. doi: 10.1017/S0954102013000576
- Hawes, I., Sumner, D.Y., Andersen, D.T., Jungblut, A.D., and Mackey, T.J. 2013. Timescales of growth response of microbial mats to environmental change in an ice-covered Antarctic lake. *Biology* 2: 151-176. doi:10.3390/biology2010151
- Hoehler, T.M., Bebout, B.M., and Des Marais, D.J. 2001. The role of microbial mats in the production of reduced gases on the early Earth. *Nature* 412(6844): 324-327.
- Howard-Williams, C., and Hawes, I. 2007. Ecological processes in Antarctic inland waters: interactions between physical processes and the nitrogen cycle. *Antarctic Science* 19(2): 205-217. doi: 10.1017/S0954102007000284
- Howard-Williams, C., Priscu, J.C., and Vincent, W.F. 1989. Nitrogen dynamics in two Antarctic streams. *Hydrobiologia* 172: 51-61.
- Huiskes, A.H.L., Gremmen, N.J.M., Bergstrom, D.M., Frenot, Y., Hughes, K.A., Imura, S., Kiefer, K., Lebouvier, M., Lee, J.E., Tsujimoto, M., Ware, C., Van de Vijver, B., and Chown, S.L. 2014. Aliens in Antarctica: Assessing transfer of plant propagules by human visitors to reduce invasion risk. *Biological Conservation* 171: 278-284.

- Jones, C.G., Lawton, J.H., and Shachak, M. 1994. Organisms as ecosystem engineers. *Oikos* 69(3): 373-386.
- Kemp, M.J., and Dodds, W.K. 2001. Spatial and temporal patterns of nitrogen concentrations of pristine and agriculturally-influenced prairie streams. *Biogeochemistry* 53: 125-141.
- Kennicutt II, M.C., Chown, S.L., Cassano, J.J., Liggett, D., Massom, R., Peck, L.S., Rintoul, S.R., Storey, J.W.V., Vaughan, D.G., Wilson, T. J., and Sutherland, W.J. 2014. Polar research: Six priorities for Antarctic science. *Nature* 512: 23-5. doi: 10.1038/512023a
- Konfirst, M.A., Sjunneskog, C., Scherer, R.P., and Doran, P.T. 2011. A diatom record of environmental change in Fryxell Basin, Taylor Valley, Antarctica, late Pleistocene to present. *Journal of Paleolimnology* 46: 257-272. doi: 10.1007/s10933-011-9537-6
- Lionard, M., Péquin, B., Lovejoy, C., and Vincent, W.F. 2012. Benthic cyanobacterial mats in the high Arctic: multi-layer structure and fluorescence responses to osmotic stress. *Frontiers in Microbiology* 3(140). doi: 10.3389/fmicb.2012.00140
- McIntyre, P.B., Flecker, A.S., Vanni, M.J., Hood, J.M., Taylor, B.W., and Thomas, S.A. 2008. Fish distributions and nutrient cycling in streams: Can fish create biogeochemical hotspots? *Ecology* 89: 2335-2346.
- McKnight, D.M., Niyogi, D.K., Alger, A.S., Bomblies, A., Conovitz, P.A., and Tate, C.M. 1999. Dry Valley Streams in Antarctica: ecosystems waiting for water. *BioScience* 49(12): 985-995.
- McKnight, D.M., Runkel, R.L., Tate, C.M., Duff, J.H., and Moorhead, D.L. 2004. Inorganic N and P dynamics of Antarctic glacial meltwater streams as controlled by hyporheic exchange and benthic autotrophic communities. *Journal of the North American Benthological Society*. 23: 171-188.
- Mueller, D.R., and Vincent, W.F. 2006. Microbial habitat dynamics and ablation control on the Ward Hunt Ice Shelf. *Hydrologic Processes* 20: 857-876. doi: 10.1002/hyp.6113
- Niyogi, D.K., Tate, C.M., McKnight, D.M., Duff, J.H., and Alger, A.S. 1997. Species composition and primary production of algal communities in Dry Valley streams in Antarctica: Examination of the functional role of biodiversity. In Lyons WB, Howard Williams C, Hawes I, Eds. *Ecosystem processes in Antarctic ice-free landscapes*. Rotterdam: Balkema, 171-179.
- O'Neill, T.A., Balks, M.R. and López-Martínez, J. 2013. Visual recovery of desert pavement surfaces following impacts from vehicle and foot traffic in the Ross Sea region of Antarctica. *Antarctic Science* 25(4): 514-530. doi: 10.1017/S0954102012001125

- Paerl, H.W., Pinckney, J.L., and Steppe, T.F. 2000. Cyanobacterial-bacterial mat consortia: examining the functional unit of microbial survival and growth in extreme environments. *Environmental Microbiology* 2(1): 11-26.
- Papineau, D., Walker, J.J., Mojzsis, S.J., and Pace, N.R. 2005. Composition and structure of microbial communities from stromatolites of Hamelin Pool in Shark Bay, Western Australia. *Applied and Environmental Microbiology* 71(8): 4822. doi: 10.1128/AEM.71.8.4822-4832.2005.
- Pertierra, L.R., Lara, F., Tejedó, P., Quesada, A., and Benayas, J. 2013. Rapid denudation processes in cryptogamic communities from Maritime Antarctica subjected to human trampling. *Antarctic Science* 25: 318-328. doi: 10.1017/S095410201200082X
- Pla-Rabes, S., Toro, M., Van de Vijver, B., Rochera, C., Villaescusa, J.A., Camacho, A., and Quesada, A. 2013. Stability and endemicity of benthic diatom assemblages from different substrates in a maritime stream on Byers Peninsula, Livingston Island, Antarctica: the role of climate variability. *Antarctic Science* 25(2): 254-269. doi: 10.1017/S0954102012000922
- Quesada, A., Fernández-Valiente, E., Hawes, I., and Howard-Williams, C. 2008. Benthic primary production in polar lakes and rivers. In Vincent, W.F., and Laybourn-Parry, J., Eds. *Polar Lakes and Rivers: Limnology of Arctic and Antarctic Aquatic Ecosystems*. New York, NY: Oxford University Press, 179-196.
- Roberts, D., and McMinn, A. 1996. Relationships between surface sediment diatom assemblages and water chemistry gradients in saline lakes of the Vestfold Hills, Antarctica. *Antarctic Science* 8(4): 331-341.
- Schirrmeister, B.E., de Vos, J.M., Antonellic, A., and Bagheri, H.C. 2013. Evolution of multicellularity coincided with increased diversification of cyanobacteria and the Great Oxidation Event. *Proceedings of the National Academy of Sciences* 110(5): 1791-1796. doi: 10.1073/pnas.1209927110
- Spaulding, S.A., McKnight, D.M., Stoermer, E.F., and Doran, P.T. 1997. Diatoms in sediments of perennially ice-covered Lake Hoare, and implications for interpreting lake history in the McMurdo Dry Valleys of Antarctica. *Journal of Paleolimnology* 17: 403-420.
- Spaulding, S., Van de Vijver, B., Hodgson, D., McKnight, D., Verleyen, E., and Stanish, L. 2010. Diatoms as indicators of environmental change in Antarctic and subantarctic freshwaters. In Smol, J.P., and Stoermer, E.F., Eds. *The diatoms: applications for the environmental and earth sciences*, 2nd ed. Cambridge, UK: Cambridge University Press, 267-286.
- Stal, L. J. 2000. Cyanobacterial mats and stromatolites. In Whitton, B.A. and Potts, M., Eds. *The ecology of cyanobacteria: their diversity in time and space*. Dordrecht, Netherlands: Kluwer Academic Press, 61-120.

- Stanish, L.F., Kohler, T.J., Esposito, R.M.M., Simmons, B.L., Nielsen, U.N., Wall, D.H., Nemergut, D.R., and McKnight, D.M. 2012. Extreme streams: flow intermittency as a control on diatom communities in meltwater streams in the McMurdo Dry Valleys, Antarctica. *Canadian Journal of Fisheries and Aquatic Sciences* 69(8): 1405-1419.
- Stanish, L.F., Nemergut, D.R., and McKnight, D.M. 2011. Hydrologic processes influence diatom community composition in Dry Valley streams. *Journal of the North American Benthological Society* 30: 1057-1073. doi: 10.1899/11-008.1
- Tanabe, Y., Ohtani, S., Kasamatsu, N., Fukuchi, M., and Kudoh, S. 2010. Photophysiological responses of phytobenthic communities to the strong light and UV in Antarctic shallow lakes. *Polar Biology* 33: 85-100.
- Tin, T., Fleming, Z.L., Hughes, K.A., Ainley, D.G., Convey, P., Moreno, C.A., Pfeiffer, S., Scott, J., and Snapes, I. 2009. Impacts of local human activities on the Antarctic environment. *Antarctic Science* 21(1): 3-33. doi: 10.1017/S0954102009001722
- Treonis, A.M., Wall, D.H. and Virginia, R.A. 1999. Invertebrate biodiversity in Antarctic dry valley soils and sediments. *Ecosystems* 2(6): 482-492.
- Villeneuve V., Vincent, W.F., and Kómarek, J. 2001. Community structure and microhabitat characteristics of cyanobacterial mats in an extreme high Arctic environment: Ward Hunt Lake. *Nova Hedwigia* 123: 199–224
- Vincent, W.F. 2000. Cyanobacterial dominance in the polar regions. In Whitton, B.A. and Potts, M., Eds. *The ecology of cyanobacteria: their diversity in time and space*. Dordrecht, Netherlands: Kluwer Academic Publisher, 321-340.
- Vincent, W.F., Castenholz, R.W., Downes, M.T., and Howard-Williams, C. 1993a. Antarctic cyanobacteria - light, nutrients, and photosynthesis in the microbial mat environment. *Journal of Phycology* 29(6): 745-755. doi: 10.1111/j.0022-3646.1993.00745.x
- Vincent, W.F., Downes, M.T., Castenholz, R.W., and Howard-Williams, C. 1993b. Community structure and pigment organisation of cyanobacteria-dominated microbial mats in Antarctica. *European Journal of Phycology* 28: 213-221.
- Vincent, W.F., Gibson, J.A.E., Pienitz, R., Villeneuve, V., Broady, P.A., Hamilton, P.B., and Howard-Williams, C. 2000. Ice shelf microbial ecosystems in the high Arctic and implications for life on Snowball Earth. *Naturwissenschaften* 87(3): 137-141. doi: 10.1007/s001140050692
- Vincent, W.F., and Howard-Williams, C. 1986. Antarctic stream ecosystems: physiological ecology of a blue-green algal epilithon. *Freshwater Biology* 16: 219-233. doi: 10.1111/j.1365-2427.1986.tb00966.x
- Vincent, W.F., and Howard-Williams, C. 2000. Life on Snowball Earth. *Science* 287: 2421.

- Vincent, W.F., Mueller, D.R., and Bonilla S. 2004. Ecosystems on ice: the microbial ecology of Markham Ice Shelf in the high Arctic. *Cryobiology* 48: 103–112.
- Vincent, W.F., and Quesada, A. 2012. Cyanobacteria in high latitude lakes, rivers and seas. In Whitton, B.A., Ed. *Ecology of cyanobacteria II: their diversity in space and time*. Dordrecht, Netherlands: Springer Science & Business Media, 371-385.
- Walsh, J.E. 2009. A comparison of Arctic and Antarctic climate change, present and future. *Antarctic Science* 21(3): 179-188.
- Warnock, J.P., and Doran, P.T. 2013. Distribution of silicious-walled algae in Taylor Valley, Antarctica lakes. *International Journal of Geosciences* 4: 688-699. doi: 10.4236/ijg.2013.44064
- Whittaker, T.E., Hall, B.L., Hendy, C.H., and Spaulding, S.A. 2008. Holocene depositional environments and surface-level changes at Lake Fryxell, Antarctica. *The Holocene* 18(5): 775-786. doi: 10.1177/0959683608091797

CHAPTER II

RECOVERY OF ANTARCTIC STREAM EPILITHON FROM SIMULATED SCOURING EVENTS

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ABSTRACT

Microbial mats are common in polar streams and often dominate benthic biomass. Climate change may be enhancing the variability of stream flows in the Antarctic, but so far studies investigating mat responses to disturbance have been limited in this region. Mat regrowth was evaluated following disturbance by experimentally scouring rocks from an ephemeral McMurdo Dry Valley stream over two summers (2001–02 and 2012–13). Mats were sampled at the beginning and resampled at the end of the flow season. In 2012–13, mats were additionally resampled mid-season along with previously undisturbed controls. In 2001–02 rocks regained 47% of chlorophyll *a* and 40% of ash-free dry mass by the end of the summer, while in 2012–13 rocks regrew 18% and 27%, respectively. Mat stoichiometry differed between summers, and reflected differences in biomass and discharge. *Oscillatoria* spp. were greatest on scoured rocks and *Phormidium* spp. on undisturbed rocks. Small diatoms *Humidophila* and *Fistulifera* spp. increased throughout the summer in all mats, with the latter more abundant in scoured communities. Collectively, these data suggest that mats are variable intra-annually, responsive to hydrology and require multiple summers to regrow initial biomass once lost. These results will aid the interpretation of long-term data, as well as inform Antarctic Specially Managed Area protocols.

INTRODUCTION

Microbial mats, visibly conspicuous biofilms covering the surfaces of terrestrial and aquatic sediments and cobbles, are common in physically and chemically stressed environments, and may account for the majority of biomass in polar freshwaters (Vincent and Howard-Williams 1986, Hawes and Howard-Williams 1998). These communities have high levels of endemism (Vyverman et al. 2010) and are primarily composed of filamentous cyanobacteria from genera *Oscillatoria* Vaucher ex Gomont, *Leptolyngbya* Anagnostidis & Komárek, *Wilmottia* Strunecký, Elster & Komárek and *Microcoleus* Desmazières ex Gomont (Alger et al. 1997), along with aerophilic diatoms that live at lower densities (Esposito et al. 2008). Benthic mats are abundant in the thalweg of streams (Alger et al. 1997). The mats are vertically stratified with high concentrations of chlorophyll *a* (Chl-*a*) in lower layers and have high concentrations of accessory pigments in upper layers, producing a vivid coloration which may be an adaptation to reduce the harmful effects of radiation (Bonilla et al. 2009).

Mats flourish in the McMurdo Dry Valleys (MDV) of Antarctica and persist as a freeze-dried crust during winter months. Stream flow is produced from glacial melt during the 4–10 weeks of summer (McKnight et al. 1999) and mats are reactivated within as little as 20 minutes after rehydration (Vincent and Howard-Williams 1986). Once activated, mats may cover a large portion of the stream bed (Alger et al. 1997) and are hotspots for biogeochemical cycling (Gooseff et al. 2004). The MDV streams have negligible grazing activity (Treonis et al. 1999), minimal lateral inputs of water and allochthonous organic material (Gooseff et al. 2011), and experience relatively uniform diel radiation in summer due to 24 hour sunlight. Collectively, this lack of convoluting factors makes MDV streams an ideal location to study how microbial mats interact with their physical environment.

Stream flow is variable in magnitude over the course of a summer. In MDV streams, the hydrograph predictably peaks on a diel cycle which may elevate discharge by orders of magnitude (Cullis et al. 2014). Interannual variability is also significant and the low discharges of the 1990s were associated with a cool period in the MDV (Doran et al. 2002). This trend was interrupted in 2001–02 with a high discharge ‘flood’ year (Doran et al. 2008). Flow has remained elevated since, punctuated with several other high flow summers (Nielsen et al. 2012). With higher flows, sediment loads may increase and substrata may mobilize, leading to the scour and transport of microbial mats (Howard-Williams et al. 1986, Hawes and Howard-Williams 1998). The McMurdo Dry Valleys Long-Term Ecological Research (MCMLTER) program has monitored mats over the last two decades. The hydrologic regime has been shown to regulate mat biomass (Stanish et al. 2011), transport (Cullis et al. 2014) and species composition (Stanish et al. 2011, 2012). However, for these communities, the effects of discrete disturbances have not been explicitly tested as for other desert streams (e.g. Fisher et al. 1982, Davie et al. 2012).

Although protected in various ways, the MDV are nonetheless projected to be both indirectly and directly influenced by human activity in the coming decades. As the ozone hole ameliorates, Continental Antarctica is projected to warm (Walsh 2009), aligning with trends already observed on the Antarctic Peninsula (Richard et al. 2013). Stream flow may increase from greater glacial melt and high flow summers could create disturbances by providing ‘pulse events’ (Nielsen et al. 2012). There may also be increased physical disturbances associated with direct anthropogenic activity in MDV due to increased numbers of visitors. Because of the slow estimated growth rates (Vincent and Howard-Williams 1986), mats could be susceptible to human disturbance such as trampling, although the known or potential human impacts are limited and have not been measured despite 60 years of research in the MDV.

In this study, two questions were addressed: i) how does microbial mat biomass recover from a scouring disturbance over different flow seasons? ii) Do these events have observable effects on elemental composition and algal community structure? Microbial mat recovery from simulated disturbance treatments was monitored to understand the impact that physical disturbances have on the colonization, structure and subsequent development of algal communities in these habitats. The results of this study may be used to help interpret long-term trends, explain spatial differences in elemental composition and guide policy for Antarctic Specially Managed/Protected Areas (ASMAs and ASPAs, www.mcmurdodryvalleys.aq) and organizations such as the International Association of Antarctic Tour Operators (IAATO, www.iaato.org).

METHODS

Site description

The MDV are the largest ice free area in Antarctica (~ 4800 km²) and are located along the coast of McMurdo Sound in south Victoria Land. Because of the unique nature of this region, the MDV are managed within an ASMA intended to minimize conflicting uses and help to protect sensitive geological and biological features. During the continual sunlight of summer months (November to January) air temperatures range from -10 to 5°C, and meltwater from alpine, piedmont and terminal glaciers form streams that flow into permanently ice-covered, closed-basin lakes on the valley floors. The MDV are extremely arid and receive < 50 mm water equivalent annually as snowfall, which primarily sublimates (reviewed by Gooseff et al. 2011). Stream solute concentrations reflect weathering reactions in the hyporheic zone and biogeochemical processes occurring in the cyanobacterial mats (Gooseff et al. 2004).

Green Creek (-77.624108, 163.060101) is located in Taylor Valley, ~ 12 km from the coast and ~ 1.2 km in length with a shallow gradient and an intermediate sized cobble pavement substratum (Figure 1). Cyanobacterial mats grow throughout its length, generating some of the highest levels of biomass reported in the MDV (Alger et al. 1997). Green Creek drains a glacial melt pond, thus seasonal variability in flow regime is lower than in other dry valley streams that may experience abrupt termination in flow following cooling temperatures, such as on cloudy days. This stream was chosen as the study site because the Taylor Valley Visitor Zone is located near its headwaters, the only tourist destination for cruise ship helicopter passengers in MDV (O'Neill et al. 2013), and it has also been the site of several experiments (i.e. Gooseff et al. 2004, Stanish et al. 2011). Furthermore, Green Creek discharge, biology and chemistry has been monitored by the MCMLTER program since 1993–94 using field and analytical methods described in Stanish et al. (2011). As a result, chemical and biological components of Green Creek are comparatively well studied.

Experimental design

To test how mats recolonize substrata over time, the regrowth of cyanobacterial mats was characterized on rocks taken upstream of the MCMLTER algal transect and downstream of the Taylor Valley Visitor Zone over two summers. These locations were chosen for mat epilithon sampling because these rock communities are potentially trampled by human foot-traffic crossing the stream. The first regrowth experiment took place during the 2001–02 summer, which coincidentally was the highest flow season on record (Doran et al. 2008). A second experiment took place over the 2012–13 summer, which had flows that were lower in magnitude. In both seasons, epilithic mat material was collected ~ 1 week after the onset of stream flow,

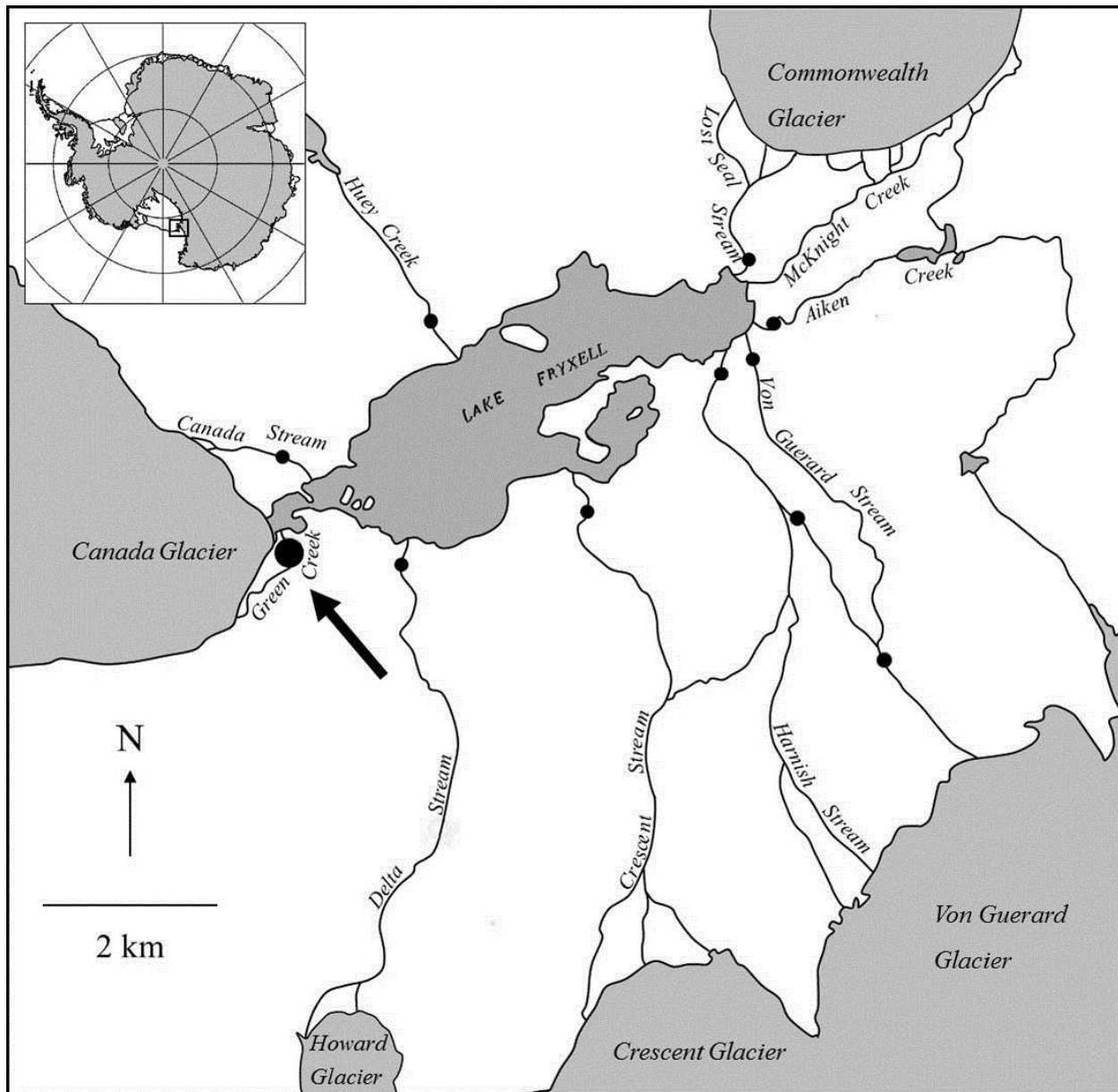


Figure 1. Detail of the Lake Fryxell basin within Taylor Valley, Antarctica. The black circles indicate gaging stations operated by the MCMLTER, and the black arrow points to the Green Creek study site.

allowing microbial communities to reactivate from the dormant state before the first sampling period.

In both experiments, 30 rocks were removed from the stream bed early in the season (day 0, 13 December 2001 and 12 December 2012), taking care not to disturb untreated substrata.

While rocks were mostly selected without bias, those that were big enough to accumulate measureable growth after several weeks but not so large that removal would affect the stream morphology were chosen (average exposed rock area $\sim 118 \text{ cm}^2$). Substrata were uniformly covered by a thick ($\sim 0.5 \text{ cm}$) orange mat. The mat material on top of each rock was removed with a toothbrush and rinsed into a container with stream water. The resulting slurry was transferred to a bottle or Whirlpack[®] bag and kept chilled and away from light until processed in the laboratory within 24 hours. The rocks were numbered, fitted with aluminium foil to measure surface area, returned to the same location in the stream and marked with surveying flags.

For 2001–02, the same rocks were resampled to measure regrowth at the end of the summer as flow began to slow (day 43, 25 January 2002), utilizing the same methods described above. Samples were not taken midway through the 2001–02 summer due to logistical problems associated with the high consistent flow. For 2012–13, half of the previously sampled rocks were resampled on day 22 (3 January 2013, $n = 15$) and the other half on day 38 (19 January 2013, $n = 15$). On each of these days an additional 15 rocks that had not been previously manipulated were sampled. These previously unsampled rocks were taken from the immediate vicinity of the resampled rocks and served as a control to measure background growth.

In 2001–02, all mat samples were filtered onto precombusted, preweighed Whatman[®] GF/F glass fibre filters and were immediately frozen and stored until analysis. Fifteen samples were analysed for ash-free dry mass (AFDM). The other 15 samples were cut in half and analysed for Chl-a or other elemental (carbon:nitrogen:phosphorus) content (final $n = 14$ for both Chl-a and stoichiometry). In 2012–13, each rock sample was split quantitatively into four aliquots for Chl-a, AFDM, stoichiometry and algal community composition by homogenizing the entire sample and splitting by volume. The AFDM and Chl-a aliquots were filtered onto

ashed, preweighed Whatman[®] GF/F filters and immediately frozen until analysis. The algal community aliquot was promptly preserved in ~ 5% formalin solution and shipped to the University of Colorado, at room temperature.

Biomass

For 2001–02, Chl-a was analysed by grinding and extracting the filters in 90% buffered acetone, centrifuging the extracts and analysing the supernatant using the trichromatic method (Strickland and Parson 1972). For 2012–13, Chl-a was measured by extracting samples in 90% buffered acetone for 24 hours and analysed on a Turner 10-AU Fluorometer (Welschmeyer 1994). The AFDM was determined by drying samples at 55°C until a constant dry mass was achieved, ashing filters at 450°C for 4 hours and rewetting (Steinman et al. 1996). Resulting AFDM and Chl-a estimates were scaled to the surface area of the rock of origin, which was calculated by applying a regression of known foils weights to known foil area (Steinman et al. 1996). An autotrophic index (AI) was calculated by dividing Chl-a values with corresponding AFDM. Percent organic material was calculated by dividing AFDM by the total sample mass. All biomass analyses were performed in Crary Laboratory at McMurdo Station.

Stoichiometry

The C:N:P aliquots were dried in an oven at 50–55°C, homogenized and ground to a fine powder. The %C and %N was measured using a Carlo Erba 1500 Elemental Analyzer (CE Instruments, Wigan) for 2001–02 samples, and a FlashEA[®] 1112 Organic Elemental Analyzer (Thermo Finnigan, Milan) for 2012–13 samples. The %P aliquot was ashed in a muffle furnace at 500°C for 1 hour, digested with 1N HCl and analysed as orthophosphate, with samples from

2001–02 estimated by the procedure of Smeller (1995) by Optical Emission Spectroscopy (Specto) and 2012–13 on a Lachat QuikChem 8500 Flow Injection Analyzer (Hach Company, Loveland, CO) by the Kiowa Laboratory at the University of Colorado (Boulder, CO; Murphy and Riley 1962). The resulting values were then converted to molar C:N, C:P and N:P ratios.

Community characterization

To investigate if simulated disturbance treatments had an effect on community structure, epilithic mat communities were characterized morphologically by light microscopy for the 2012–13 summer samples utilizing methods similar to Alger et al. (1997). Briefly, five samples for each treatment and date (ten for day 0, 30 in total) were randomly chosen, homogenized and a ~ 1 ml aliquot was transferred into a concave microscope slide and observed under 400x magnification. Each filament, colony or solitary cell was classified as one natural unit and identified to the lowest taxonomic designation possible (generally genus), and at least 150 units were counted for each sample. Diatoms were always counted as one unit, even if forming a colony, and the viability of each frustule (live or dead) was documented. Live diatoms were classified as those that had protoplast material remaining in the frustule at the time of preservation. After enumeration of the community was complete, the slide was scanned for several minutes for more diatoms (to increase live/dead sample size) and the percentage of live and dead diatoms encountered was then calculated.

Representative soft algal cells (in a colony, filament or solitary) were counted and measured in each field with the ocular micrometre. Dimensions for diatoms were measured if possible, but if a valve was obstructed making measurement impossible, width and length averages were taken from the Antarctic Freshwater Diatoms website

(<http://huey.colorado.edu/diatoms/about/index.php>). Valve depth was estimated for genera as follows, based on measurements during the study: 12.5 μm for *Hantzschia*, 10 μm for *Muelleria*, 5 μm for *Luticola*, 3.75 μm for *Stauroneis* and 2.5 μm for all others. Relative biovolumes of the taxonomic groups were then calculated using equations from Hillebrand et al. (1999). Komárek and Anagnostidis (2005) was the primary resource used for cyanobacterial identification. Although the *Phormidium* spp. in our samples have recently been transferred to the genus *Microcoleus* (Strunecký et al. 2013); single trichomes are referred to classically as ‘*Phormidium*’ and multiple trichomes in a sheath as ‘*Microcoleus*’ to avoid confusion.

Diatoms were further described to species by digesting another aliquot from the corresponding samples in 30% H_2O_2 with low heat and rinsed with distilled water until a neutral pH was achieved. The digested material was dried onto cover slips and mounted onto glass microscope slides with the mounting medium Zrax[®] (refractive index = 1.7; W.P. Dailey, University of Pennsylvania, Philadelphia, PA). Relative abundances of diatom species were determined using an Olympus Vanox light microscope (Japan) at 1250 \times magnification, with \geq 300 valves enumerated per slide. Diatoms were identified to species according to descriptions from Esposito et al. (2008), Kopalová et al. (2012) and the Antarctic Freshwater Diatoms website.

Flow and water chemistry

Green Creek stream flow and water temperature are continuously monitored at the outlet to the lake, and discharge was measured as part of the MCMLTER with the use of a pressure transducer logging at 15 minute intervals. Stream water was collected concurrently with each site visit throughout both summers. All water chemistry sampling and analyses were conducted

following the methods outlined in Welch et al. (2010). Briefly, raw water was collected in triple-rinsed 250 ml Nalgene[®] bottles for nutrient samples and 125 ml precombusted amber glass bottles for dissolved organic carbon (DOC). Water for nutrient analysis was filtered from the raw water sample on glass fibre filters and frozen for later analysis at the field station. Cation and anion samples were filtered with Nuclepore[™] polycarbonate membrane filters with 0.4 μ m pore size and refrigerated at 4°C. Samples for DOC were filtered and acidified using concentrated HCl and stored at 4°C for later analysis at the Crary Laboratory at McMurdo Station. All discharge and chemistry data are available at <http://www.mcmlter.org>.

Statistical Analyses

All variables that were not normally distributed were log-transformed to satisfy the assumption of normality. Pairwise *t*-tests were conducted to directly compare rock variables at initial and final time points (before and after disturbance). To test if disturbed rock variables were significantly different from controls on the same dates, or if initial or final rock variables were different between the two flow seasons (i.e. comparisons between different sample pools), means were compared with a Welch two sample *t*-test. Thirty rocks were scraped on day 0 in 2012–13, whereas 15 were sampled for regrowth and controls respectively on day 22 and 38, as well as both sample dates in 2001–02. To avoid differences in the number of observations, the regrowth on individual rocks from day 0 were directly compared with later dates from 2012–13. The rocks sampled for regrowth on day 22 are ‘group A’ and rocks resampled on day 38 are ‘group B’. When final and initial values between the 2001–02 and 2012–13 summers were compared, only rock data from day 0 that corresponded with the rock regrowth on day 38 were used (group B).

For community data, non-Euclidean Redundancy Analyses (RDA) were created to visualize differences between algal and diatom communities between treatments and days utilizing the vegan R package. Rare species that occurred < 5.0% by relative abundance or biovolume were removed and data were square root transformed to satisfy assumptions of normality. An extra diatom community sample was counted for a regrown mat on day 38, and was included in the multivariate analysis but not the direct comparisons of relative abundances as outlined above for biomass and stoichiometry. Significance of sample day and treatment were evaluated by permutational multivariate analysis of variance (PERMANOVA), significance at $\alpha = 0.05$. Additionally, identical analyses were performed for diatom communities, excluding *Fistulifera pelliculosa* (Brébisson ex Kützing) Lange-Bertalot whose origin and ecology are ambiguous (Stanish et al. 2012).

All statistical analyses were performed using the R statistical environment, version 2.13.0 (R Core Team 2014).

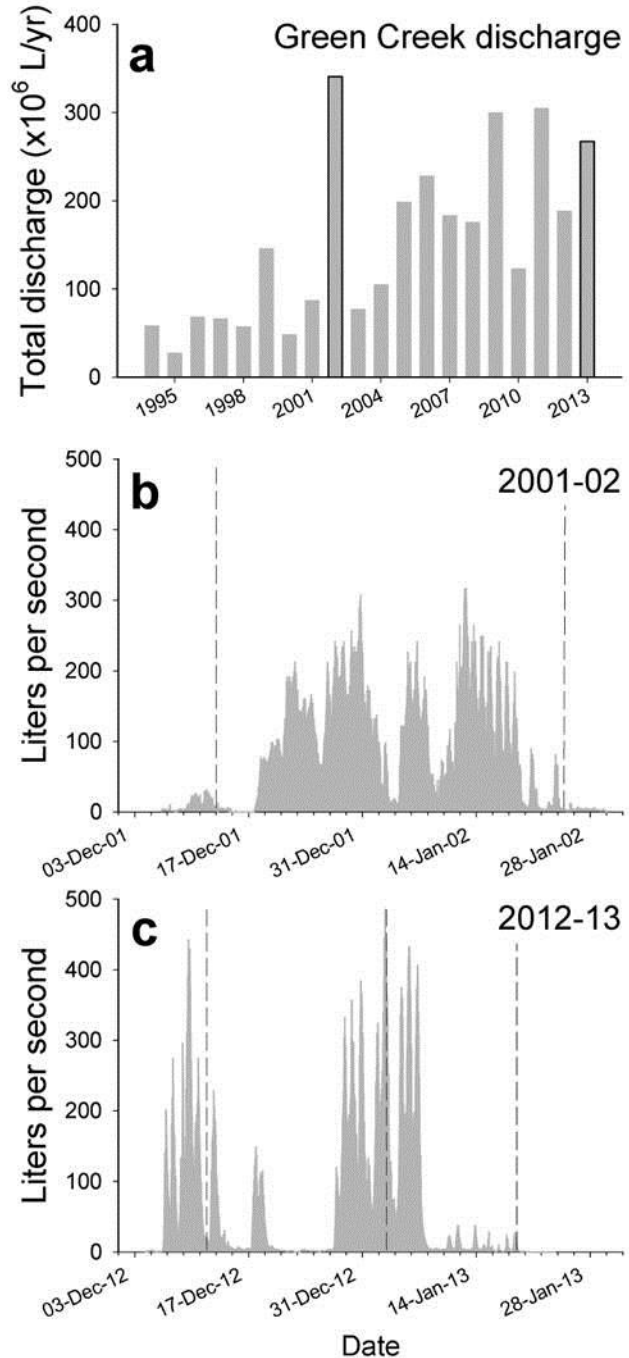
RESULTS

Discharge, mats and nutrients

The summer of 2001–02, regarded as the ‘flood year’, is the highest flow season in Green Creek on record (Figure 2a, Doran et al. 2008). There were consistent high discharges throughout the year (Figure 2b). The average flow was 72 l s^{-1} and the maximum flow recorded was 315 l s^{-1} . The total discharge was $3.41 \times 10^8 \text{ l}$. Nutrient concentrations for 2001–02 summer averaged $10.48 \text{ } \mu\text{g N-NO}_3^- \text{ l}^{-1}$, $2.16 \text{ } \mu\text{g N-NO}_2^- \text{ l}^{-1}$, $4.81 \text{ } \mu\text{g N-NH}_4^+ \text{ l}^{-1}$ and $4.40 \text{ } \mu\text{g P-soluble reactive phosphorus (SRP) l}^{-1}$ (Table 1).

Flows for 2012–13 were more intermittent compared to 2001–02, and the stream experienced prolonged periods without flow, though at discrete intervals exhibited punctuated

Figure 2. Top: a. total calculated discharge taken from the Green Creek gage (F9) for each summer for 1993-94 through 2012-13. Darkened bars indicated summers highlighted in this study. Middle and bottom: Hydrograph of the continuous discharge measurements taken from the Green Creek stream gage (F9) during the a. 2001-02 and b. 2012-13 summers. Dotted lines indicate dates epilithon was sampled.



high flow events (Figure 2c). The average discharge for 2012–13 summer was 61 l s^{-1} and the maximum flow recorded was 485 l s^{-1} . Despite the intermittent nature, high flows brought the total discharge to $2.67 \times 10^8 \text{ l}$, which is the third highest total discharge for this stream since the 1993–94 summer. Nutrient concentrations averaged $15.87 \mu\text{g N-NO}_3^- \text{ l}^{-1}$, $1.31 \mu\text{g N-NO}_2^- \text{ l}^{-1}$, $< 5 \mu\text{g N-NH}_4^+ \text{ l}^{-1}$ (detection limit) and $3.85 \mu\text{g P-SRP l}^{-1}$ (Table 1).

Over the last two decades of microbial mat monitoring in Green Creek, orange mat biomass from the downstream algal transect has been higher on average than epilithon measured in this study, ranging from 1.07 to $11.16 \mu\text{g cm}^{-2}$ for Chl-a (Figure 3a) and 3.08 to 16.99 mg cm^{-2} for AFDM (Figure 3b). For the 2012–13 summer, orange mat biomass averaged $4.29 \mu\text{g Chl-a cm}^{-2}$ and $6.40 \text{ mg AFDM cm}^{-2}$. Similarly, 2011–12 biomass averaged

Table 1. Values for physical and chemical parameters opportunistically sampled from Green Creek streamwater during the 2001-02 and 2012-13 summers.

Date	Time	N-NO ₃ ⁻ (µg/L)	N-NO ₂ ⁻ (µg/L)	N-NH ₄ ⁺ (µg/L)	P-SRP (µg/L)	pH	Water temp (°C)	SC (µS)	DOC (µg/L)	Si (µg/L)	SO ₄ ²⁻ (µg/L)	Alk (meq/L)
11 Dec 2001	16:30	14.3	<2.0	<2.0	2.3	NA	9.2	31.1	200	570	1370	NA
13 Dec 2001	14:50	8.6	<2.0	<2.0	2.6	7.1	4.0	38.8	160	680	1380	0.22
21 Dec 2001	12:00	12.8	<2.0	3.7	4.5	8.1	7.2	38.4	<100	360	1470	0.20
1 Jan 2002	23:00	10.8	<2.0	2.3	7.0	7.3	2.7	25.2	<100	300	760	0.23
25 Jan 2002	16:00	6.0	2.8	14.2	5.6	NA	2.2	24.5	<100	820	830	0.32
11 Dec 2012	12:45	36.1	2.1	<5.0	4.1	6.9	2.5	31.5	200	309	1122	0.18
18 Dec 2012	12:19	17.5	1.0	<5.0	3.5	6.9	5.9	27.3	320	410	898	0.22
26 Dec 2012	15:30	13.1	2.1	<5.0	4.0	7.3	8.4	45.5	615	940	936	0.38
2 Jan 2013	21:15	16.3	<0.7	<5.0	6.3	7.5	4.6	24.4	<100	277	745	0.20
11 Jan 2013	11:21	11.5	1.9	<5.0	2.7	7.2	7.2	36.3	206	635	781	0.37
15 Jan 2013	13:00	1.9	<0.7	<5.0	3.5	8.0	7.5	34.9	113	621	934	NA
23 Jan 2013	14:20	14.8	2.2	<5.0	2.9	NA	NA	NA	134	799	855	0.31

7.24 µg Chl-a cm⁻² and 7.43 mg AFDM cm⁻². Average nutrient ratios for orange mats measured in this year were C:N = 9.55, C:P = 74.34 and N:P = 7.77. Mat samples were not taken during the 2001–02 summer due to challenges associated with sustained high flows, but averaged 9.73 µg Chl-a cm⁻² and 10.02 mg AFDM cm⁻² in 2000–01, and 7.28 µg Chl-a cm⁻² and 3.12 mg AFDM cm⁻² in 2002–03 (Figure 3a & b).

Comparison of mat recovery between two summers

Mat biomass measured as epilithon was substantially less than the thick mats monitored as part of the MCMLTER. Initial Chl-a measurements averaged 1.18 µg Chl-a cm⁻² for 2001–02 and 1.00 µg Chl-a cm⁻² for 2012–13, and were not statistically different (Figure 4a). The final Chl-a concentrations were significantly lower in 2012–13 (Welch's *t*-test, *t* = 4.49, *df* = 26.94, *P* < 0.01), and averaged 0.18 µg cm⁻² in 2012–13 compared to 0.56 µg cm⁻² in 2001–02 (Figure 4a). Final rock samples had significantly less Chl-a than initial samples in 2001–02 (Paired *t*-test, *t* = 4.19, *df* = 12, *P* < 0.01) and 2012–13 (Paired *t*-test, *t* = -5.49, *df* = 14, *P* < 0.01). The AFDM was not significantly different at the beginning of the two seasons and averaged 1.50 and 1.15 mg AFDM cm⁻² for 2001–02 and 2012–13, respectively (Figure 4b). The AFDM values were lower

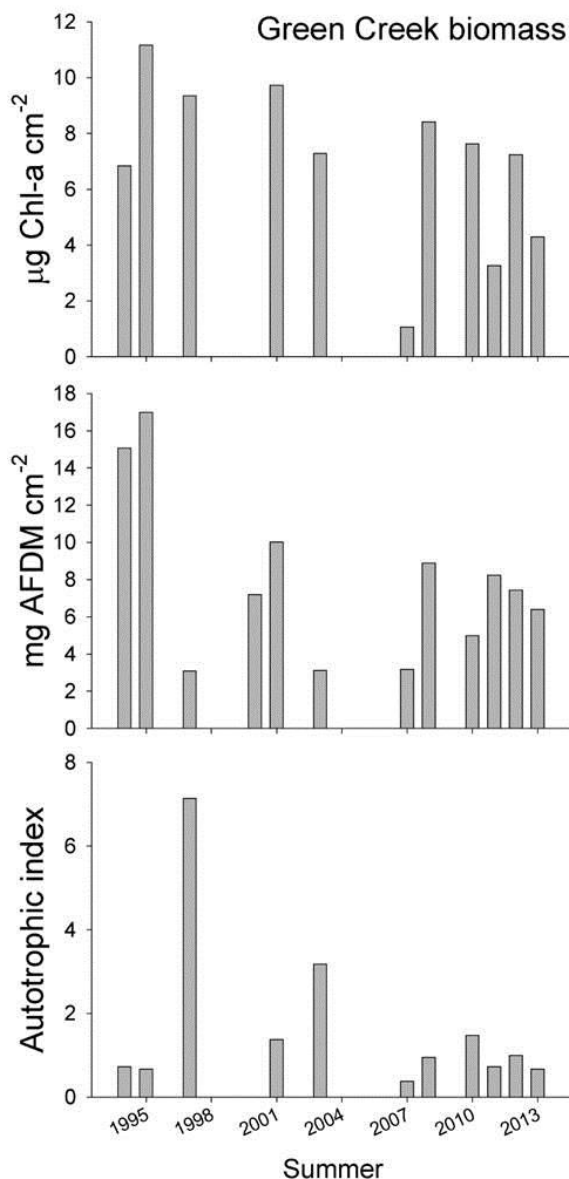


Figure 3. Top to bottom: a. average Chl-a, b. ash-free dry mass (AFDM), and c. autotrophic index (AI = Chl-a:AFDM) for monitored orange mats sampled at the downstream Green Creek transect as part of the MCMLTER for each summer, 1993-94 through 2012-13. Where bars are absent samples were not taken. See Stanish et al. (2011) for detailed collection and analytical methods.

at the end of 2012–13, averaging 0.31 mg cm^{-2} compared to 0.61 mg cm^{-2} for 2001–02 (Welch's *t*-test, $t = 2.61$, $df = 19.99$, $P = 0.02$). Lastly, mat AFDM was significantly reduced from the initial to the final sampling in both 2001–02 (Paired *t*-test, $t = 4.01$, $df = 14$, $P < 0.01$) and 2012–13 (Paired *t*-test, $t = -5.92$, $df = 14$, $P < 0.01$). The percent regrowth was greater in 2001–02 compared to 2012–13 for Chl-a (47% and 18%) and AFDM (40% and 27%).

Initial C:N ratios of mats averaged 10.02 and 10.04 for 2001–02 and 2012–13,

respectively, and were not statistically different (Figure 4c). However, the final ratios in 2012–13 were significantly greater than the final ratios in 2001–02, averaging 9.19 and 11.45, respectively (Welch's *t*-test, $t = -7.23$, $df = 23.68$, $P < 0.01$). Within seasons, initial mats had greater C:N ratios than final samples in 2001–02 (Paired *t*-test, $t = 3.75$, $df = 12$, $P < 0.01$), and final mats had greater C:N ratios than initial in 2012–13 (Paired *t*-test, $t = 5.04$, $df = 13$, $P < 0.01$, Figure 4c). In contrast, C:P ratios were only marginally greater for 2001–02 initial material, averaging

Rock regrowth between two summers

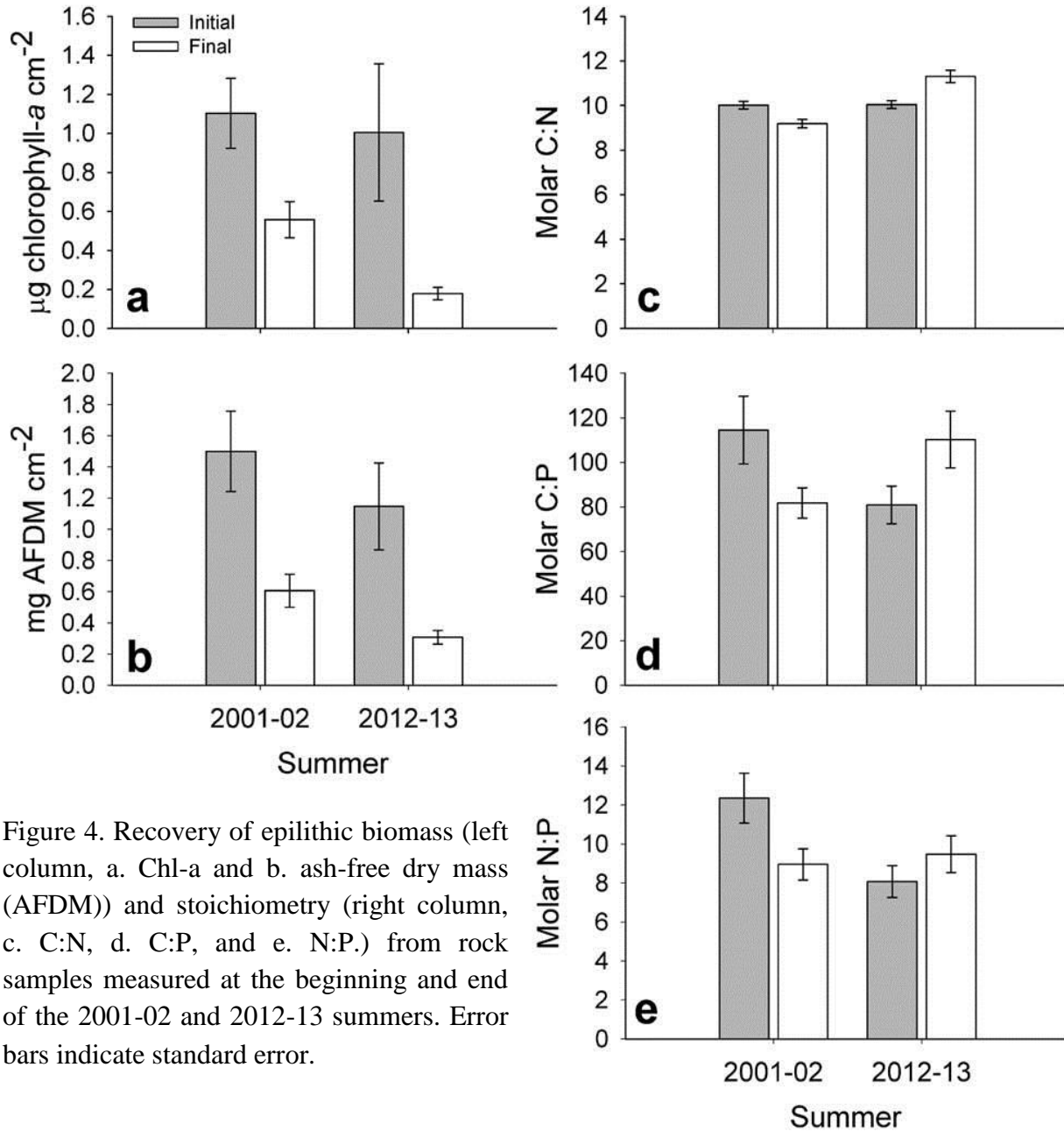


Figure 4. Recovery of epilithic biomass (left column, a. Chl-a and b. ash-free dry mass (AFDM)) and stoichiometry (right column, c. C:N, d. C:P, and e. N:P.) from rock samples measured at the beginning and end of the 2001-02 and 2012-13 summers. Error bars indicate standard error.

114.50 versus 80.92 for 2012–13 (Welch's *t*-test, $t = 1.93$, $df = 20.53$, $P = 0.07$, Figure 4d). Final C:P ratios were marginally greater in 2012–13 than 2001–02 (Welch's *t*-test, $t = -1.98$, $df = 19.87$, $P = 0.06$). Within summers, initial C:P ratios were greater than final in 2001–02 (Paired *t*-test, $t = 3.17$, $df = 13$, $P = 0.01$), but in 2012–13 final ratios were significantly greater than initial (Paired *t*-test, $t = 4.27$, $df = 13$, $P < 0.01$, Figure 4d). These patterns were the same for N:P ratios,

though less pronounced (Figure 4e). The N:P ratios were significantly greater in the initial mats from 2001–02 compared to 2012–13 (Welch's t -test, $t = 2.82$, $df = 22.35$, $P = 0.01$), but there was no significant difference between the 2001–02 and 2012–13 final mats (Figure 4e). Mat N:P was significantly greater in initial mats than resampled mats in 2001–02 (Paired t -test, $t = 3.81$, $df = 13$, $P < 0.01$), but significantly greater in resampled mats in 2012–13 compared to initial mats (Paired t -test, $t = 2.72$, $df = 13$, $P = 0.02$, Figure 4e).

Biomass and stoichiometry over the 2012-13 summer

The differences between group A and group B on day 0 were not significant for any variable. Chlorophyll a was greatest in the middle of the growing season (day 22), with the control samples averaging $1.53 \mu\text{g Chl-}a \text{ cm}^{-2}$ (Figure 5a). Experimentally scoured rocks had significantly lower Chl- a concentrations than control rocks on day 22 (Welch's t -test, $t = 13.10$, $df = 25.05$, $P < 0.01$) and day 38 (Welch's t -test, $t = 8.33$, $df = 24.77$, $P < 0.01$), and averaged $0.09 \mu\text{g Chl-}a \text{ cm}^{-2}$ on day 22 and $0.18 \mu\text{g Chl-}a \text{ cm}^{-2}$ on day 38 (Figure 5a). Compared to initial values, 11% of the Chl- a was regrown by day 22 and 18% by day 38. Averaged values for AFDM increased throughout the sampling period in the control mats and ranged from 1.15 (primary group B) to 1.60 (control 2, Figure 5b). Again, cleaned rocks had significantly less AFDM than control rocks on day 22 (Welch's t -test, $t = -9.43$, $df = 14.22$, $P < 0.01$) and day 38 (Welch's t -test, $t = -5.10$, $df = 14.86$, $P < 0.01$). Mats that were cleaned of mat material on day 0 regrew 12% of their biomass compared to the initial values by day 22 and 27% of initial biomass by day 38, averaging 0.16 and $0.31 \text{ mg AFDM cm}^{-2}$, respectively (Figure 5b).

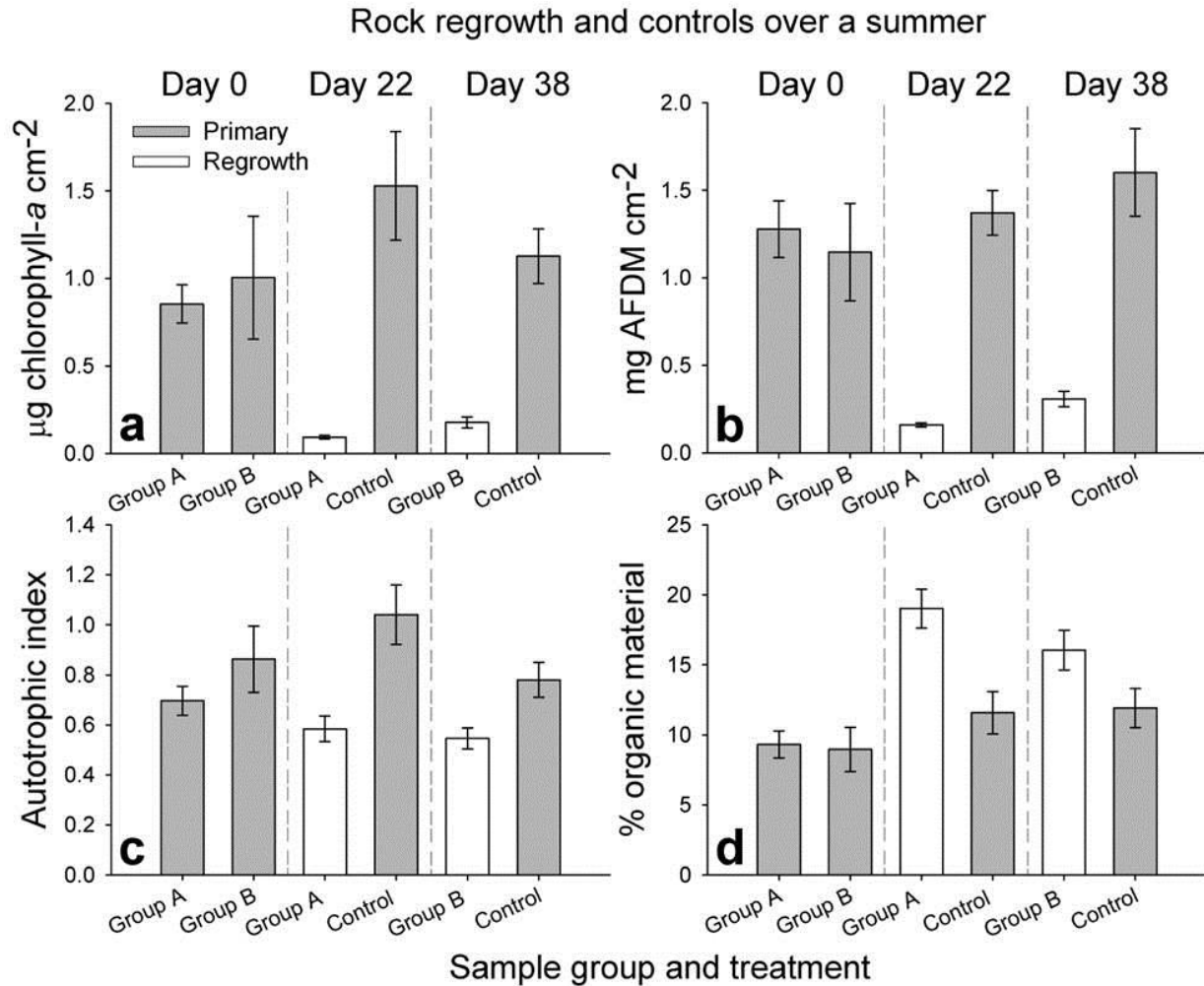


Figure 5. Biomass as a. Chl-a, b. ash-free dry mass (AFDM), c. autotrophic index (AI=Chl-a:AFDM), and d. the percent organic material for each group of rocks and associated controls for the 2012-13 summer. Grey bars indicate the primary samples, and white bars indicate regrowth. Samples are arranged by date. Error bars indicate standard error.

As for Chl-a, the AI was greatest on day 22 for undisturbed mats (Figure 5c). Experimentally scoured rocks had significantly lower AI values than controls on day 22 (Welch's *t*-test, $t = -4.27$, $df = 26.90$, $P < 0.01$) and day 38 (Welch's *t*-test, $t = 2.86$, $df = 22.99$, $P = 0.01$, Figure 5c). The average percent organic content for undisturbed samples increased throughout the growing season, ranging from 9.0% (primary group B) to 11.9% (control 2; Figure 5d). However, cleaned rocks had a greater percent organic content, with the greatest

values measured on day 22 (19.0%), decreasing by day 38 (16.1%). Organic content at day 22 was significantly greater than all background samples (Figure 5d). At day 38, percent organic content was only significantly greater than the primary mats from day 0 (Figure 5d).

The %C, %N and %P were greatest in the regrowth from group A on day 22 (Figure 6a–c). However, the nutrient content of resampled rocks was not significantly different from controls on day 22 or day 38. Molar C:N ratios of all samples were above the Redfield ratio of ~ 7, and increased throughout the summer, ranging from 10.0 on day 0 (both group A and B) to 11.8 on day 38 (control 2, Figure 6d). Material from regrowth had significantly greater C:N ratios than control samples on day 22 (Welch's t -test, $t = 2.26$, $df = 27.20$, $P = 0.03$) but not on day 38 (Figure 6d). Molar C:P ratios were approximately at or above the Redfield ratio of ~ 106, and ranged from 105 on day 38 (control 2) to 125 on day 22 (group A), but regrowth was not significantly different from controls on either sample date (Figure 6e). For molar N:P ratios, all values were below the Redfield ratio of 16, and ranged from 8.1 (primary group B) to 11.2 (control 1, Figure 6f). Similar to C:P, average N:P values were greatest on day 22, but regrowth was not significantly different than controls on either day 22 or 38 (Figure 6f).

Microbial community structure

Epilithic communities were dominated by genera *Nostoc* Vaucher ex Bornet & Flahault, *Phormidium* (solitary *Microcoleus*), *Oscillatoria* and *Wilmottia* (Figure 7a). Minor genera (compiled in 'other' category) included representatives from *Calothrix* C.Agardh ex Bornet & Flahault, *Leptolyngbya*, *Microcoleus* (colonial), *Nodularia* Mertens ex Bornet & Flahault, *Pseudoanabaena* Lauterborn and *Schizothrix* Kützing ex Gomont. The disturbance treatment had

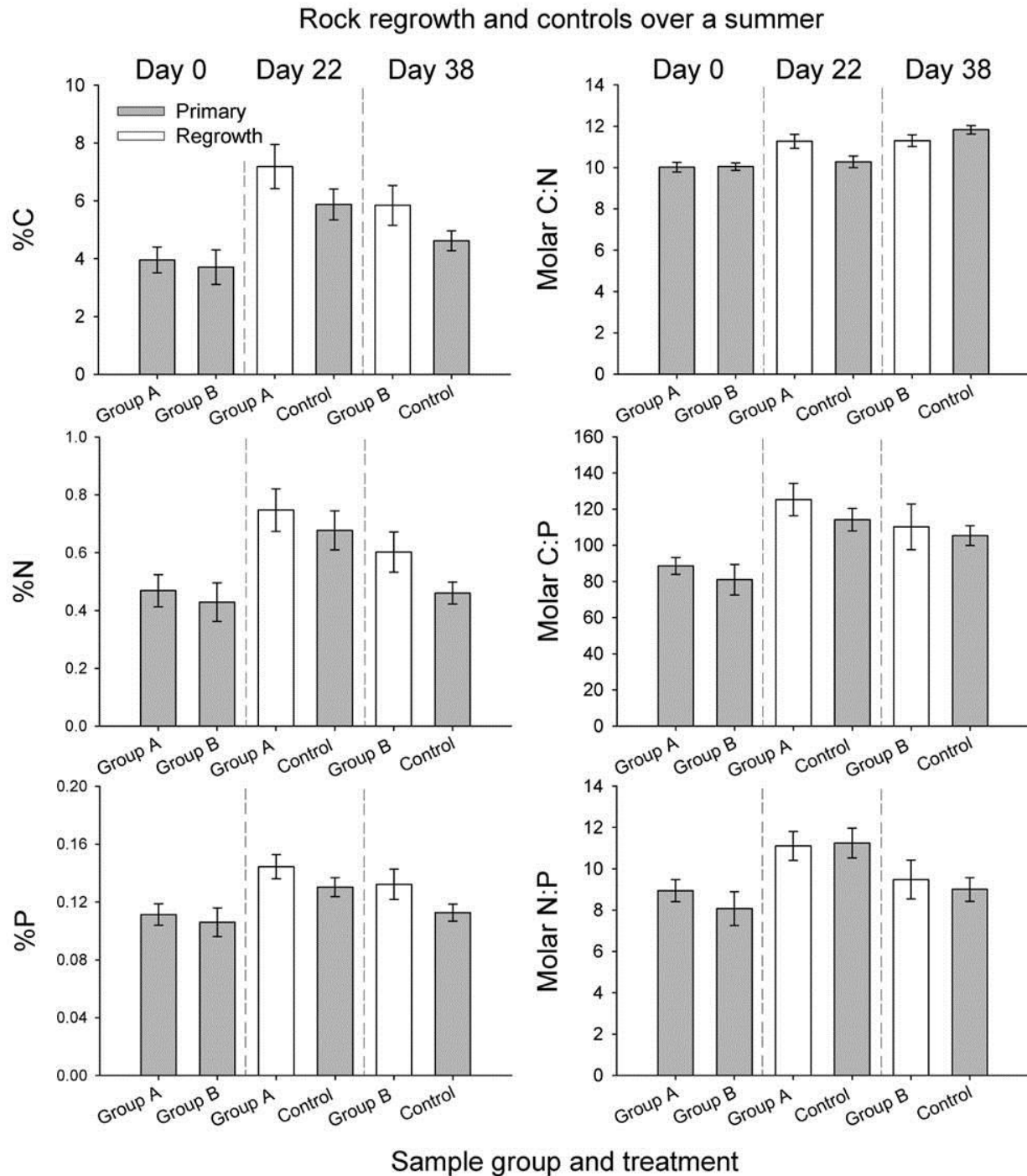


Figure 6. Nutrient composition of epilithon for each group of rocks and associated controls for the 2012-13 summer. Left column: a. %C, b. %N, and c. %P. Right column: molar e. C:N, f. C:P, and g. N:P. Grey bars indicate the primary samples, and white bars indicate regrowth. Samples are arranged by date. Error bars indicate standard error.

visible effects on community structure, with the proportion of *Oscillatoria* spp. being greater on substrata that had been disturbed (mean \pm standard error, $45.2\% \pm 5.8$ vs $31.6\% \pm 3.3$) and *Phormidium* spp. more scarce in biovolume on disturbed substrata ($11.0\% \pm 2.8$ vs $36.4\% \pm 4.3$).

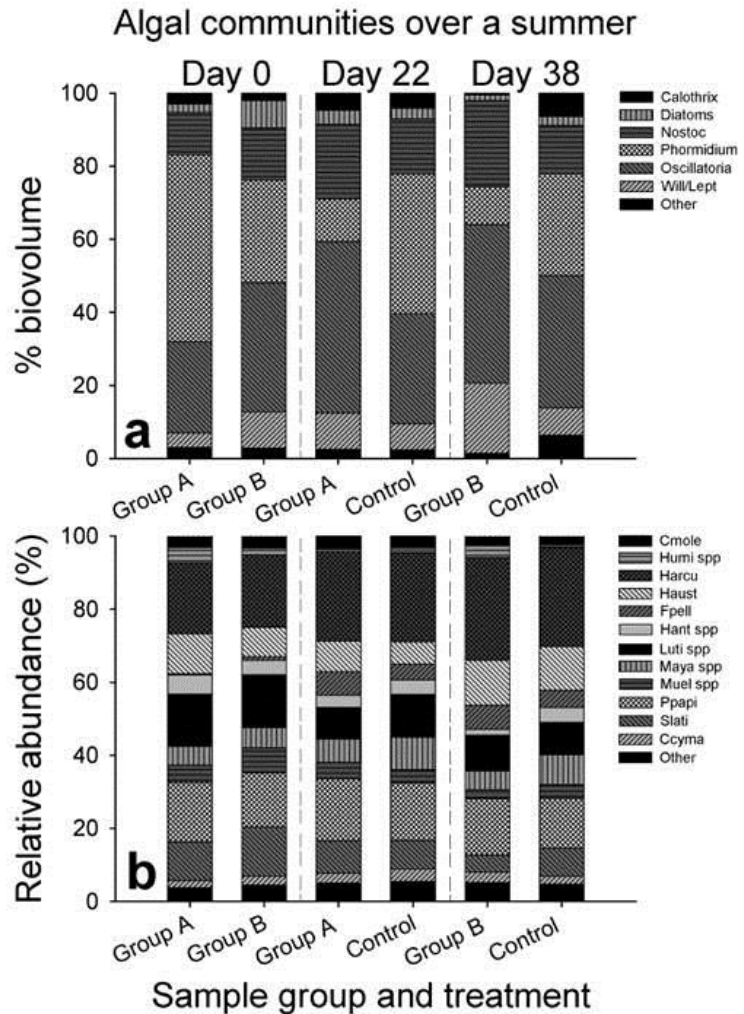
Diatoms comprised a small proportion of the communities, 0–27% of the total biovolume, with an average of 3.4% (± 0.97). The live/dead status of diatoms was also variable throughout the flow year and by treatment. Diatoms from group A averaged 54% viable ($n = 43$) and group B 41% ($n = 65$) on day 0. By day 22, 29% of diatoms had intact chloroplasts in group A ($n = 18$), as opposed to the control group with 76% ($n = 44$). On the last sample date, group B had 47% viable diatom frustules ($n = 28$) and the control had 40% ($n = 35$). It is possible that diatom biovolume and viability was prejudiced by our inability to see smaller frustules, as larger cells from genera *Stauroneis* Ehrenberg, *Luticola* D.G.Mann, *Hantzschia* Grunow and *Muelleria* (Frenguelli) Frenguelli were the most commonly encountered. These were small members of the communities by relative abundance, with small frustules from genera *Psammothidium* L.Buhtkiyarova & Round and *Humidophila* Lowe, Kociolek, Johansen, Van de Vijver, Lange-Bertalot & Kopalová being the most numerous (see below).

Consistent with other studies from the continent, diatom community diversity was low in comparison with the rest of the Antarctic region, with only 35 species from 17 genera observed. Communities were largely similar throughout the experiment, although there were some notable exceptions with some taxa (Figure 7b). *Stauroneis latistauros* Van de Vijver & Lange-Bertalot averaged 16% of the community on day 0, but was reduced by $\sim 50\%$ on subsequent days. *Muelleria* spp. showed the same pattern, with an average of 7% of the community belonging to the genus on day 0, decreasing by 50% in subsequent days. *Fistulifera pelliculosa* exhibited the opposite trend; contributing $< 1\%$ of the community on day 0, and growing in relative abundance

Figure 7. Stacked bar graph of the a. overall epilithic community by percent biovolume and the b. relative abundance of major groups of diatoms. For the composite figure, *Wilmottia spp.* and *Leptolyngbya spp.* are combined. For the relative abundances of diatoms, taxonomic abbreviations are as follows: Cmole = *Craticula molestiformis*, Humi spp = *Humidophila spp.*, Harcu = *H. arcuata*, Haust = *H. australis*, Fpell = *Fistulifera pelliculosa*, Hants pp = *Hantzschia spp.*, Luti spp = *Luticola spp.*, Maya spp = *Mayamaea spp.*, Muel spp = *Muelleria spp.*, Ppapi = *Psammothidium papilio*, Slati = *Stauroneis latistauros*, and Ccyma = *Chamaepinnularia cymatopleura*.

over the course of the flow season, with the greatest abundances in disturbed mat communities. *Luticola* spp. decreased in relative abundances

over the course of the season, with less *Luticola* present in disturbed communities. *Psammothidium papilio* (D.E. Kellogg, Stuiver, T.B. Kellogg & Denton) Van de Vijver & Kopalová remained relatively constant throughout time and treatments with the exception of day 22, where they made up 17% of the communities on average. *Hantzschia* spp. also showed no visible change over time or treatment. Diatom communities from epilithon were very similar to those sampled from orange mats over the same season, and were dominated by *Humidophila* spp., *P. papilio*, *S. latistauros* and *Luticola austroatlantica* Van de Vijver, Kopalová, Spaulding & Esposito.



The results from permutation tests (PERMANOVA) suggest treatment (primary versus regrowth) was a highly significant factor in structuring epilithic communities ($F = 5.40$, $P < 0.01$). However, sample day was not a significant factor for the epilithic communities as measured by percent biovolume of cyanobacteria and diatoms ($F = 1.56$, $P = 0.15$). When diatom relative abundances were tested, samples were significantly different as a function of disturbance treatment ($F = 2.34$, $P = 0.02$), as well as the date sampled ($F = 2.89$, $P < 0.01$). When *F. pelliculosa* was removed from the dataset, sample day remained significant ($F = 2.07$, $P = 0.01$) but not the effect of treatment ($F = 1.47$, $P = 0.13$).

To investigate the drivers of this variability, epilithic communities were plotted in an RDA as a function of treatment (Figure 8a). For the entire epilithic community, *Phormidium* drives most of the variation along axis 1 and 2, and is nearest to many of the primary samples, followed by *Oscillatoria* and *Nostoc* which are closer to regrowth. *Calothrix* explained variation in axis 2, aligning with primary samples. When diatom communities were plotted as an RDA, *F. pelliculosa* drives most of the treatment effects, aligning closely with the samples from regrown mats (Figure 8b). Diatom communities further separated along both axes as a function of date sampled. RDA axis 1 explained 24.5% of the variation, and was driven by abundances of *Stauroneis*, *Muelleria* and *Luticola* spp. on one side, and *Humidophila* spp. and *F. pelliculosa* on the other (Figure 9a). RDA axis 2 explained 13.4% of the variation, and driven mainly by *H. arcuata* (Heiden) Lowe, Kociolek, Johansen, Van de Vijver, Lange-Bertalot & Kopalová and *H. australis* (Van de Vijver & Sabbe) Lowe, Kociolek, Johansen, Van de Vijver, Lange-Bertalot & Kopalová on the top, with *F. pelliculosa* on the bottom. When *F. pelliculosa* was removed, these patterns remained, though day 22 and 38 samples became more similar to day 0 (Figure 9b).

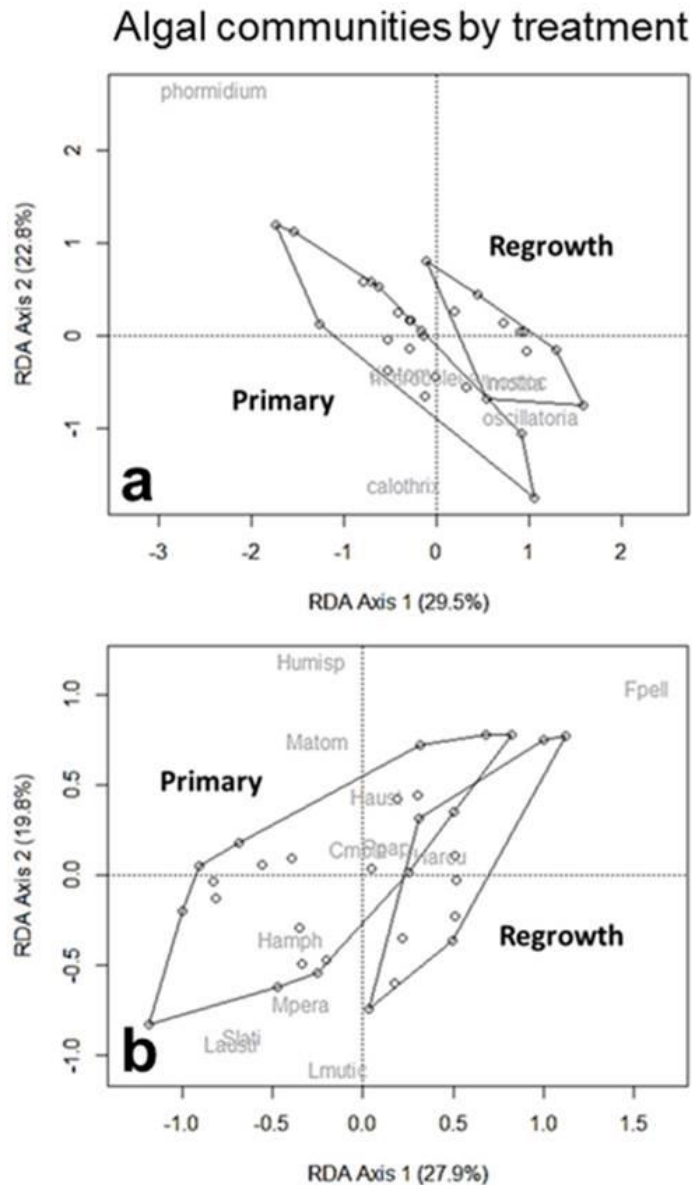


Figure 8. Redundancy analysis (RDA) of a. composite and b. diatom communities separated by disturbance treatment. Abbreviations for diatom taxa are as follows: Cmole = *Craticula molestiformis*, Fpell = *Fistulifera pelliculosa*, Hamph = *Hantzschia amphioxys*, Humisp = *Humidophila spp.*, Hausc = *H. arcuata*, Haust = *H. australis*, Laustr = *Luticola austroatlantica*, Lmutic = *L. muticopsis*, Matom = *Mayamaea atomus*, Mpera = *Muelleria peraustralis*, Ppapi = *Psammothidium papilio*, and Slati = *Stauroneis latistauros*.

DISCUSSION

Microbial mats dominate biomass in Antarctic streams, and the factors that regulate their abundance are important ecological considerations for the MDV, especially under increasing human pressures and changing environmental conditions. In this study, epilithic

AFDM and Chl-a were substantially reduced after a scouring disturbance and regrowth rates ranged from ~ 20–50% over the summer. Based on these results, it follows that epilithic mats in Green Creek require multiple flow seasons without further perturbation before returning to the prior biomass (Vincent and Howard-Williams 1986, Hawes and Howard-Williams 1998), placing the MDVs on the high end of the recovery spectrum compared to mid-latitude streams (Fisher et al. 1982, Davie et al. 2012). Furthermore, disturbed communities had reduced proportions of *Phormidium* spp. and elevated *Oscillatoria* spp. The effects of disturbance were

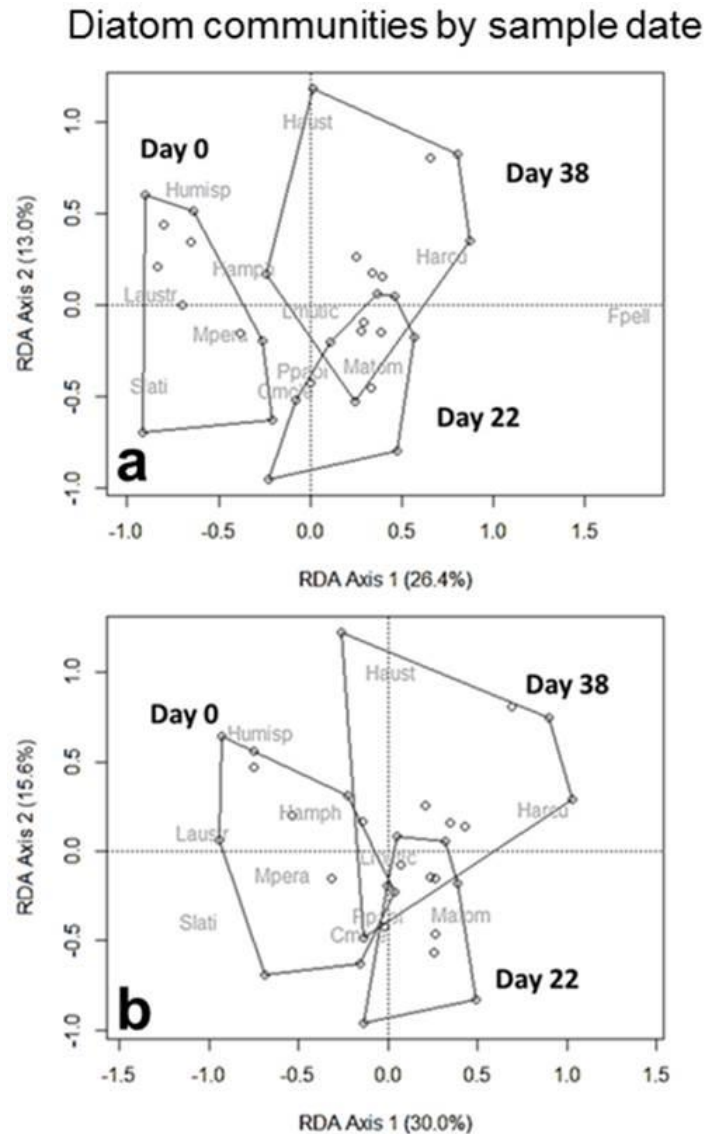
Figure 9. Redundancy analysis (RDA) of diatom communities as a function of sample date with a. all species and b. excluding the small diatom, *Fistulifera pelliculosa*. Abbreviations for diatom taxa are given in the caption for Figure 8.

less apparent for nutrient ratios and diatom community structure. Rather, there was temporal variation in the nutrient stoichiometry and diatom community structure as the growing season progressed.

Biomass

Elevated flows may stimulate in-stream mat growth through decreasing cellular boundary layers and increasing nutrient delivery (Biggs et al. 1998). While mats

are adapted to withstand drying, periods of low desiccating flows result in reduced productivity (Wyatt et al. 2014). For these reasons, increases in growing season length (i.e. days with stream flow) accompanying climate warming may ultimately increase mat biomass in the MDV. However, stream microbial mats also exhibit losses due to scouring, where a threshold is met in which turbulence or sediment loads removes mat material from substrata (Hawes and Howard-Williams 1998). Mat biomass in several streams was previously shown to decrease after the high



flow summer of 2001–02 (Stanish et al. 2011), and the transport of mat material has been modelled as a function of diel hydrology in another Fryxell basin stream (Cullis et al. 2014).

In this study, more biomass was recovered during the summer with a higher total discharge (2001–02). This is probably because the initial set of 2001–02 samples were taken in the midst of low steady discharges and final samples were taken after some higher flows at the end of the summer. As a result, cobble substrata remained wetted for the majority of this flow season. In contrast, the initial samples in 2012–13 were taken after some potentially scouring discharges (see peaks in Figure 2c) and the final samples were taken during a time of prolonged low flow which may have desiccated substrata outside the thalweg. It may follow that the variability of future hydrologic regimes, rather than magnitude alone, dictates whether biomass will accumulate or be reduced in MDV streams, and testing multiple hydrologic indices over a broad spatial scale will be necessary to evaluate this prediction.

Previous investigators in Maritime Antarctic streams have demonstrated variable Chl-a and AFDM measurements over the course of a summer (Davey 1993, Pizarro and Vincour 2000), probably due to variability in physical and chemical characteristics over the longitudinal gradient of the stream and over the flow season. Davey (1993) demonstrated that spatial and temporal heterogeneity were important factors for biomass, as Chl-a concentrations differed by stream habitat sampled (channel or margin). In our study, day 22 stands out as having the greatest biomass during the 2012–13 summer (as well as the greatest proportion of viable diatoms), which coincided with a period of high flow. This illustrates that MDV streams are intra- as well as inter-seasonally dynamic ecosystems.

Stoichiometry

Trends between the initial and final nutrient ratios over the two summers were opposite. All stoichiometric ratios decreased from initial to final in 2001–02, while increasing over in 2012–13. As for biomass, this may be due to increased nutrient delivery associated with higher (non-scouring) discharges (Biggs et al. 1998). Since the first summer had more consistent flow (and terminated later), it follows that more nutrient resources were made available for uptake and assimilation. Conversely in 2012–13, where flow was regularly disrupted and ceased earlier, fewer nutrients were taken up, and those that were assimilated may have been used for maintenance rather than reproduction, especially at the end of the summer when flows were low. Similarly, the release of exudates and proteins that can occur with desiccation (Wyatt et al. 2014) may have direct stoichiometric consequences by changing the protein to carbohydrate ratios in epilithon.

Patterns in stoichiometry may be partially explained by corresponding trends in biomass. For example, as AFDM increased throughout the 2012–13 summer, %C also increased as reflected in C:N and C:P ratios. As Chl-a is a nitrogen rich molecule (four N atoms each), the peak in Chl-a on day 22 may help explain the concurrent increase in N:P. The C:N ratios were also higher in the 2012–13 summer compared to 2001–02, the latter of which had greater Chl-a values. The higher initial C:P and N:P ratios in 2001–02 versus the lower final values may indicate that growing cyanobacterial mats contain more cellular P allocated for reproductive material than the established mats. Therefore, it is expected that stoichiometry, as well as biomass, has varied both within and across summers over the course of the MCMLTER program. Elucidating relationships between regrowth and stoichiometry will be important in predicting long-term trends in elemental mass balance in the MDV.

Microbial communities

Diatom communities were remarkably stable after disturbance, despite marked differences in AFDM and Chl-a. The biggest differences were detected by date rather than treatment. The high resilience of these communities may reflect an evolved ability to persist despite periodic scour. Stanish et al. (2011) reported that after the flood year of 2001–02, many monitored stream diatom communities remained unchanged from the flood, while *Diademesmis contenta* var. *parallela* (J.B.Petersen) Hamilton (now *Humidophila arcuata* (Lange-Bertalot) Lowe, Kociolek, Johansen, Van de Vijver, Lange-Bertalot & Kopalová) and *Psammothidium* sp#1 (*P. papilio*) increased markedly in Green Creek after the flood year. On the other hand, *Luticola austroatlantica* and *L. muticopsis* (Van Heurck) D.G. Mann both decreased in relative abundance. This may suggest that diatom communities may have a sort of ‘tipping point’ with regard to disturbance and these Green Creek communities may already reflect a disturbed status, not having fully recovered from the changes observed during the high flow summer of 2001–02 (Stanish et al. 2011).

Most of the differences observed in diatom communities by disturbance treatment were driven by *Fistulifera pelliculosa*, which is a small, lightly silicified species hypothesized to drift in from seepages and ‘playa’ areas (Stanish et al. 2012). However, Kopalová et al. (2012) found the similar *F. saprophila* (Lange-Bertalot & Bonik) Lange-Bertalot was abundant in streams and not observed in seepages. More work should be done to understand the ecology of this important indicator species. The relative abundance of other diatom species increased or declined over the course of the flow season in Green Creek, despite never being physically disturbed, though overall differences were small. Interestingly, soft algae communities showed larger differences between treatments, with low abundances of *Phormidium* spp. on disturbed rocks, although

control communities remained similar through the summer. This suggests that MDV diatoms may not always reflect changes in the epilithon community structure. Collectively, these insights are important considerations for interpreting living (Stanish et al. 2011, Stanish et al. 2012) and ancient material (Konfirst et al. 2011).

Conclusions and further considerations

Microbial mats could be susceptible to direct physical human disturbances due to their slow regeneration rates. Our finding that epilithic mats require multiple seasons to regrow the initial biomass from one discrete disturbance event may suggest that annual perturbations (or multiple disturbances per year) may cumulatively suppress biomass, potentially alter the community structure and cause greater than *de minimis* impacts at least in some cases.

While this study concentrates on epilithic mats prone to trampling by visitors using rocks to cross wet areas near the Taylor Valley Visitor Zone, extrapolation of the data to all of the MDV microbial mats monitored as part of the MCMLTER should be done with caution. First, trampling may not lead to the complete removal of epilithon as presented here, and regrowth estimates may differ with a gradient of disturbance intensities. Secondly, a diversity of mats occupy the MDV, exhibiting variable thicknesses, utilizing different habitats and differing in the dominant taxa. Consequently, resistance to change and recovery time vary for different mat types. Lastly, Green Creek is a favourable habitat with a moderate gradient, low sediment load and extensive stone pavement. As a result, cyanobacterial mats may regrow more quickly here than in other MDV streams. Further study will be necessary to fully evaluate both realized and potential human impacts on mat communities in Antarctica.

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REFERENCES

- Alger, A.S., McKnight, D.M., Spaulding, S.A., Tate, C.M., Shupe, G.H., Welch, K.A., Edwards, R., Andrews, E.D., and House, H.R. 1997. Ecological processes in a cold desert ecosystem: the abundance and species distribution of algal mats in glacial meltwater streams in Taylor Valley, Antarctica. Institute of Arctic and Alpine Research Occasional Paper 51.
- Biggs, B.J.F., Goring, D.G., and Nikora V.I. 1998. Subsidy and stress responses of stream periphyton to gradients in water velocity as a function of community growth form. *Journal of Phycology* 34: 598-607.
- Bonilla, S., Rautio, M., and Vincent, W.F. 2009. Phytoplankton and phytobenthos pigment strategies: implications for algal survival in the changing Arctic. *Polar Biology* 32: 1293-1303. doi: 10.1007/s00300-009-0626-1
- Cullis, J.D.S., Stanish, L.F., and McKnight, D.M. 2014. Diel flow pulses drive particulate organic matter transport from microbial mats in a glacial meltwater stream in the McMurdo Dry Valleys. *Water Resources Research* 50. doi:10.1002/2013WR014061.
- Davey, M.C. 1993. Carbon and nitrogen dynamics in a maritime Antarctic stream. *Freshwater Biology* 30: 319-330.
- Davie, A.W., Mitrovic, S.M., and Lim, R.P. 2012. Succession and accrual of benthic algae on cobbles of an upland river following scouring. *Inland Waters* 2: 89-100. doi: 10.5268/IW-2.2.441
- Doran, P. T., Priscu, J.C., Lyons, W.B., Walsh, J.E., Fountain, A.G., McKnight, D.M., Moorhead, D.L. Virginia, R.A., Wall, D.H., Clow, G.D., Fritsen, C.H., Mckay, C.P., and Parsons, A.N. 2002. Antarctic climate cooling and terrestrial ecosystem response. *Nature* 415: 517-520.
- Doran, P.T., Mckay, C.P., Fountain, A.G., Nylen, T., McKnight, D.M., Jaros, C., and Barrett,

- J.E. 2008. Hydrologic response to extreme warm and cold summers in the McMurdo Dry Valleys, East Antarctica. *Antarctic Science* 20: 499-509. doi:10.1017/S0954102008001272
- Esposito, R.M.M., Spaulding, S.A., McKnight, D.M., Van De Vijver, B., Kopalová, K., Lubinski, D., Hall, B., and Whittaker, T. 2008. Inland diatoms from the McMurdo Dry Valleys and James Ross Island, Antarctica. *Canadian Journal of Botany* 86: 1378-1392. doi: 10.1139/B08-100.
- Fisher, S.G., Gray, L.J., Grimm, N.B., and Busch, D.E. 1982. Temporal succession in a desert stream ecosystem following flash flooding. *Ecological Monographs* 52: 93-110.
- Gooseff, M.N., McKnight, D.M., Doran, P., Fountain, A.G., and Lyons, W.B. 2011. Hydrological connectivity of the landscape of the McMurdo Dry Valleys, Antarctica. *Geography Compass* 5/9: 666–681.
- Gooseff, M.N., McKnight, D.M., Runkel, R.L., and Duff, J.H. 2004. Denitrification and hydrologic transient storage in a glacial meltwater stream, McMurdo Dry Valleys, Antarctica. *Limnology and Oceanography* 49: 1884–1895.
- Hawes, I., and Howard-Williams, C. 1998. Primary production processes in streams of the McMurdo Dry Valleys, Antarctica. In Prisco, J.C., Ed. *Ecosystem Dynamics in a Polar Desert: The McMurdo Dry Valleys, Antarctica*, Antarctic Research Series Vol. 72. Washington, D.C.: American Geophysical Union, 129–140.
- Hillebrand, H., Dürselen, C., Kirschtel, D., Pollinger, U., and Zohary, T. 1999. Biovolume calculation for pelagic and benthic microalgae. *Journal of Phycology* 35: 403–424.
- Howard-Williams, C., Vincent, C.L., Broady, P.A., and Vincent, W.F. 1986. Antarctic stream ecosystems: Variability in environmental properties and algal community structure. *Internationale Revue der Gesamten Hydrobiologie und Hydrographie* 71: 511–544.
- Komárek, J., and Anagnostidis, K. 2005. Cyanoprokaryota - 2. Teil: Oscillatoriales. In Buedel, B., Krienitz, L., Gaertner, G. and Schagerl, M., Eds. *Süßwasserflora von Mitteleuropa*, Band 19/2. Heidelberg: Elsevier/Spektrum, 759.
- Konfirst, M.A., Sjunneskog, C., Scherer, R.P., and Doran, P.T. 2011. A diatom record of environmental change in Fryxell Basin, Taylor Valley, Antarctica, late Pleistocene to present. *Journal of Paleolimnology* 46: 257-272. doi: 10.1007/s10933-011-9537-6
- Kopalová, K., Veselá, J., Elster, J., Nedbalová, L., Komárek, J., and Van De Vijver, B. 2012. Benthic diatoms (Bacillariophyta) from seepages and streams on James Ross Island (NW Weddell Sea, Antarctica). *Plant Ecology and Evolution* 145: 190-208. doi: 10.5091/plecevo.2012.639
- McKnight, D.M., Niyogi, D.K., Alger, A.S., Bomblies, A., Conovitz, P.A., and Tate, C.M. 1999. Dry Valley streams in Antarctica: ecosystems waiting for water. *Bioscience* 49: 985-995.

- Murphy, J., and Riley, J.P. 1962. A modified single solution method for determination of phosphate in natural waters. *Analytica Chimica Acta* 26: 31–36.
- Nielsen, U.N., Wall, D.H., Adams B.J., Virginia R.A., Ball, B.A., Gooseff, M.N., and McKnight, D.M. 2012. The ecology of pulse events: insights from an extreme climatic event in a polar desert ecosystem. *Ecosphere* 3: 17.
- O'Neill, T.A., Balks, M.R., and López-Martínez, J. 2013. Visual recovery of desert pavement surfaces following impacts from vehicle and foot traffic in the Ross Sea region of Antarctica. *Antarctic Science* 25: 514-530. doi:10.1017/S0954102012001125
- Pizarro, H., and Vincour, A. 2000. Epilithic biomass in an outflow stream at Potter Peninsula, King George Island, Antarctica. *Polar Biology* 23: 851-857.
- R Core Team. 2014. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>.
- Richard, Y., Rouault, M., Pohl, B., Crétat, J., Duclot, I., Taboulot, S., Reason, C.J.C., Macron, C., and Buiron, D. 2013. Temperature changes in the mid- and high- latitudes of the Southern Hemisphere. *International Journal of Climatology* 33: 1948-1963.
- Smeller, J.M. 1995. Comparison of sample preparation methods for the spectrophotometric determination of phosphorus in soil and cola fly ash. *Analyst* 120: 207-210.
- Stanish, L.F., Kohler, T.J., Esposito, R.M.M., Simmons, B.L., Nielsen, U.N., Wall, D.H., Nemergut, D.R., and McKnight, D.M. 2012. Extreme streams: flow intermittency as a control on diatom communities in meltwater streams in the McMurdo Dry Valleys, Antarctica. *Canadian Journal of Fisheries and Aquatic Sciences* 69(8): 1405-1419. doi: 10.1139/f2012-022
- Stanish, L.F., Nemergut, D.R., and Mcknight, D.M. 2011. Hydrologic processes influence diatom community composition in Dry Valley streams. *Journal of the North American Benthological Society* 30: 1057-1073. doi: 10.1899/11-008.1
- Steinman, A., Lamberti, G.A., and Leavitt, P.R. 1996. Biomass and pigments of benthic algae. In Hauer, F.R., and Lamberti, G.A., Eds. *Methods in stream ecology*, 2nd ed. San Diego, CA: Academic Press, 357-379.
- Strickland, J.D.H., and Parsons, T.R. 1972. *A practical handbook of seawater analysis*, 2nd ed. Ottawa, Ontario: Fisheries Research Board of Canada Bulletin, 167.
- Strunecký, O., Komárek, J., Johansen, J., Lukešová, A., and Elster, J. 2013. Molecular and morphological criteria for revision of the genus *Microcoleus* (*Oscillatoriales*, cyanobacteria). *Journal of Phycology* 49: 1167–1180. doi: 10.1111/jpy.12128

- Treonis, A.M., Wall, D.H., and Virginia, R.A. 1999. Invertebrate biodiversity in Antarctic Dry Valley soils and sediments. *Ecosystems* 2: 482-492.
- Vincent, W.F., and Howard-Williams, C. 1986. Antarctic stream ecosystems: physiological ecology of a blue-green algal epilithon. *Freshwater Biology* 16: 219-233. doi: 10.1111/j.1365-2427.1986.tb00966.x
- Vyverman, W., Verleyen, E., Wilmotte, A., Hodgson, D., Willems, A. Peeters, K. Van De Vijver, B., De Wever, A., Leliaert, F., and Sabbe, K. 2010. Evidence for widespread endemism among Antarctic micro-organisms. *Polar Science* 4: 103-113. doi: 10.1016/j.polar.2010.03.006
- Walsh, J.E. 2009. A comparison of Arctic and Antarctic climate change, present and future, *Antarctic Science* 21: 179-188. doi: 10.1017/S0954102009001874.
- Welch, K.A., Lyons, W.B., Whisner, C., Gardner, C.B., Gooseff, M.N., McKnight, D.M., and Prisco, J.C. 2010. Spatial variations in the geochemistry of glacial meltwater streams in the Taylor Valley, Antarctica. *Antarctic Science* 22: 662-672. doi:10.1017/S0954102010000702
- Welschmeyer, N.A. 1994. Fluorometric analysis of chlorophyll a in the presence of chlorophyll b and pheopigments. *Limnology and Oceanography* 39: 1985–1992. doi:10.4319/lo.1994.39.8.1985.
- Wyatt, K. H., Rober, A.R., Schmidt, N., and Davison, I.R. 2014. Effects on desiccation and rewetting on the release and decomposition of dissolved organic carbon from benthic microalgae. *Freshwater Biology* 59: 407-416. doi:10.1111/fwb.12273

CHAPTER III
LIFE IN THE MAIN CHANNEL: LONG-TERM HYDROLOGIC CONTROL OF
MICROBIAL MAT ABUNDANCE IN MCMURDO DRY VALLEY STREAMS,
ANTARCTICA

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ABSTRACT

Given alterations in global hydrologic regime, we examine the role of hydrology in regulating stream microbial mat abundance in the McMurdo Dry Valleys, Antarctica. Here, perennial mats persist as a desiccated crust until revived by summer streamflow, which varies inter-annually, and has increased since the 1990's. We predicted high flows to scour mats, and intra-seasonal drying to slow growth. Responses were hypothesized to differ based on mat location within streams, along with geomorphology, which may promote (high coverage) or discourage (low coverage) accrual. We compared hydrologic trends with the biomass of green and orange mats, which grow in the channel, and black mats growing at stream margins for 16 diverse stream transects over two decades. We found mat biomass collectively decreased during first decade coinciding with low flows, and increased following elevated discharges. Green mat biomass showed the greatest correlations with hydrology and was stimulated by discharge in high coverage transects, but negatively correlated in low coverage due to habitat scour. In contrast, orange mat biomass was negatively related to flow in high coverage transects, but positively correlated in low coverage because of side-channel expansion. Black mats were weakly correlated with all hydrologic variables regardless of coverage. Lastly, model selection indicated the best combination of predictive hydrologic variables for biomass differed between mat types, but also high and low coverage transects. These results demonstrate the importance of

geomorphology and species composition to modeling primary production, and will be useful in predicting ecological responses of benthic habitats to altered hydrologic regimes.

INTRODUCTION

Flow is commonly referred to as the “master variable” in stream ecology (Poff et al. 1997), and is a known driving factor for epilithic biomass in streams across the globe, including temperate (Dodds et al. 2004), tropical (Kohler et al. 2012), and desert (Grimm and Fisher 1989) stream ecosystems. This effect can be manifested by the direct physical disruption of epilithic structure and function through scour and accrual (e.g. Biggs and Thomsen 1995, Biggs et al. 1998, Francoeur and Biggs 2006), as well as indirectly through influencing the flux of nutrients in the water column (Stevenson 1996, Dodds and Biggs 2002, Simon et al. 2004). With the worldwide modification of flow paths (Poff et al. 2007) and possible intensification of the hydrologic cycle (reviewed by Huntington 2006), it is important to understand how altered flow regimes may affect stream primary production (for example, Davis et al. 2013) as well as the transport of autochthonous organic material (Cullis et al. 2014).

Concurrently, the range and riverine abundance of some bloom-forming freshwater taxa have expanded due to anthropogenic modification of flow. For example, the stalked diatom *Didymosphenia geminata* (Lyngbye) M. Schmidt has become a nuisance because of the dense mats it forms (Spaulding and Elwell 2007), especially in regulated rivers and streams (Whitton et al. 2009). Although relatively unpalatable to grazers (Cullis et al. 2012), high flows may regulate its biomass through scour and mobilization of substrata (Miller et al. 2009, Cullis et al. 2012), and flow regime has been previously linked to bloom vulnerability (Kumar et al. 2009). However, streams in temperate regions typically exhibit a high degree of heterogeneity, and

convoluting factors such as seasonality, watershed variability, trophic complexity, and human influences make variable isolation and interpretations difficult. As a result, our understanding of the basic associations between geomorphology, streamflow, and mat-forming algae such as *D. geminata* remains limited (Cullis et al. 2012).

Due to their simplicity, glacial meltwater streams in the McMurdo Dry Valleys (MDV), Antarctica, provide an excellent setting for studying the relationships between flow and periphyton biomass loss and accrual (Cullis et al. 2014). Streams here flow for 4-10 weeks each summer (Fountain et al. 1999, McKnight et al. 1999) and lateral inflows and terrestrial organic inputs are almost non-existent because the surrounding terrain consists of large expanses of barren, unconsolidated alluvium (Gooseff et al. 2011). Primary production in MDV streams is dominated by four perennial microbial mat types that persist through the winter in a freeze-dried, cryptobiotic state, and are reactivated within minutes of being rehydrated (Vincent and Howard-Williams 1986, Hawes et al. 1992) even after decades without flow (McKnight et al. 2007). These mats differ taxonomically, occupy different habitats within the stream, and experience negligible grazing losses because the density of the dominant grazers, tardigrades and nematodes, is very low (Treonis et al. 1999, Virginia and Wall 1999). Because of the restricted flow season, minimal watershed influence, and simple trophic structure, the MDVs are ideal for studying physical controls on microbial mats.

In the MDVs, geomorphic characteristics of the stream channels are proposed to control the level of benthic coverage by microbial mats (McKnight et al. 1998), which is generally stable from year to year (McKnight and Tate 1997). Some stream reaches have dense microbial mats with near 100% coverage of the streambed, whereas others have only sparse patches (Howard-Williams et al. 1986, Alger et al. 1997). Stream reaches with high algal mat coverage share the

same general characteristics, exhibiting relatively low flow velocities over medium gradients (Hawes and Howard-Williams 1998), stable stone pavement substrata (McKnight et al. 1998), and low sediment loads (Howard-Williams et al. 1986, Vincent and Howard-Williams 1986). This in turn allows multiple years of growth to accumulate in the absence of sloughing. Conversely, low coverage reaches occur in deltaic areas with sandy substrata, which easily mobilize and create high sediment loads, or with uneven boulder substrata over a steep gradient, which encourages the scour of mats.

The scour and transport of mat material is an important loss mechanism in the MDVs, and was experimentally modeled by Cullis et al. (2014) as a function of discharge. Because discharge is a function of glacial melt, climatic changes may alter microbial mat biomass and transport in the MDVs. In the late 1980's, a trend of colder summers in the MDVs decreased average annual stream flow (Doran et al. 2002), possibly due to decreases in atmospheric ozone over East Antarctica (the ozone hole) resulting from past global CFC emissions (Walsh 2009). This trend was interrupted during the warm summer of 2001-2002, which remains the highest flow season on record (Doran et al. 2008). Since that summer, discharge has increased compared to the previous 10-year average, and has recently been punctuated by other high flow years in 2008-2009 and 2010-2011 (www.mcmlter.org). The cooling trend is predicted to reverse with the amelioration of the ozone hole (Arblaster and Meehl 2006, Chapman and Walsh 2007, Thompson et al. 2011), leading to warming like that already observed on the Antarctic Peninsula (Richard et al. 2013). As a result, the frequency of high flow events per season is expected to increase, although the effects of hydrologic processes on microbial mat growth and persistence over large temporal and spatial scales are not well known.

In this study, we build upon hypotheses generated by three decades of research in the MDVs and vicinity (Figure 1) and ask: 1) Do different types of mats respond similarly to different hydrologic conditions, and 2) does the geomorphology of a given stream influence these responses to hydrology? Specifically, high flow events are predicted to scour mats (Vincent and Howard-Williams 1986, Stanish et al. 2011, et al. 2014), and intra-seasonal streambed drying will slow mat growth (Hawes et al. 1992). These effects are expected to vary by mat type due to differences in habitat use and growth form (Biggs et al. 1998), with relationships most pronounced for mats utilizing the stream channel (Howard-Williams et al. 1986, Rochera et al. 2013) where flow is more consistent and resident mats may be more sensitive to desiccation and scour. Using benthic mat coverage as a proxy for shared geomorphological characteristics (gradient and substrata), we further predict that mats from high and low coverage transects should have different responses to hydrologic trends (Howard-Williams et al. 1986, Alger et al. 1997, McKnight et al. 1998). We test these hypotheses by comparing long-term trends in hydrologic variables with the biomass of different microbial mats for 16 stream transects that vary in their benthic coverage over a 20-year period.

METHODS

Description of MDV Streams and Transects

Dry Valley glacial melt is generated by the warming of the surface layer of the glacier through a solid state greenhouse effect at air temperatures as low as -5°C (Jaros 2003). Diel variation in cloud cover, sun angle, and insulation causes large flow fluctuations in the stream habitat, and discharge can vary as much as 10-fold during a 24-hour period (Conovitz et al. 1998). Because of high permeability of the alluvium, MDV streams typically have a substantial hyporheic zone

		High Flows			Low Flows		
Losses	Green	7	Scour of mats on talus, sand delta, stone pavement	X ₃	--	Desiccation of outside thalweg, hyporheic zone	--
	Orange	1, 3, 4, 10		X ₁	6		X ₇
	Black	11		--	6		X ₅
Gains	Green	8	<u>Gain habitat at stream margins, high growth rates</u>	X ₂	--	<u>Slow growth/ little scour</u>	X ₆
	Orange	3, 4, 5		X ₄	2, 9		--
	Black	4, 5		--	2		--

Figure 1. Conceptual diagram illustrating the predicted and observed mechanisms for mat biomass gains and losses under high and low flow conditions in Antarctic streams. Numbers in the boxes to the near right of each mat type indicate literature from which hypotheses were used to design our study: (1) Stanish et al. 2011, (2) Hawes et al. 1992, (3) Howard-Williams et al. 1986, (4) Vincent and Howard-Williams 1986, (5) McKnight and Tate 1997, (6) McKnight et al. 2007, (7) Hawes 1989, (8) Rochera et al. 2013, (9) Hawes and Howard-Williams 1998, (10) Cullis et al. 2014, and (11) Dodds et al. 1995. “X₁₋₇” in the boxes to the far right of each mat type indicate a significant result based on Figure 7.

that is controlled by the depth of permafrost (Cozzetto et al. 2006), water temperature (Cozzetto et al. 2013), and discharge (Conovitz et al. 1998, Koch et al. 2011), and can be observed as a damp area adjacent to the stream. As a result, the initial loss of water from the channel to the expanding hyporheic zone (Conovitz et al. 1998) can control the onset of streamflow, especially for longer streams. Stream temperature can vary from 4°C to 15°C on a diel basis, with the peak temperature controlled by solar radiation and limited by evaporative cooling (Gooseff et al. 2003, Cozzetto et al. 2013). For small streams, maximum discharges exceeded 1 m³ s⁻¹ during the warmest summer on record (2001-2002), and larger streams had bank-full floods for several days. In contrast, during the cold summers that were typical during the cooling period of the 1990’s, many small streams exhibited minimal flow (less than 0.01 m³ s⁻¹) for only a few weeks or produced no measurable discharge (House et al. 1995, Jaros 2003).

Four mat types (for brevity: green, orange, red, and black) are generally recognized in the MDVs based on their appearance and dominant taxa, but also their habitat preference within the stream (Alger et al. 1997, McKnight et al. 1998). Green mats occur in small patches or as streamers attached to rocks, and are dominated by the chlorophyte genus *Prasiola* Meneghini (Alger et al. 1997). Orange and red mats are composed of filamentous cyanobacteria from genera *Oscillatoria* Vaucher ex Gomont, *Leptolyngbya* Anagnostidis & Komárek, and *Microcoleus* Desmazières ex Gomont, and can form cohesive benthic mats up to 5 mm thick in the thalweg of streams (Vincent et al. 1993, Alger et al. 1997, Niyogi et al. 1997). These mats are vertically stratified (see, Bonilla et al. 2005, Lionard et al. 2012) with a distinct orange or red upper layer enriched in accessory pigments, and an under layer with greater chlorophyll-a content and photosynthetic activity (Vincent et al. 1993). While red mats are taxonomically similar to orange mats, they have a dense, rubbery outer surface and are sparsely distributed. Lastly, black mats are formed by *Nostoc* Vaucher ex Bornet & Flahault, and are found at the stream margins where moisture is available from the hyporheic zone (Alger et al. 1997).

The 16 monitored stream transects are located in 12 streams within three lake basins in Taylor Valley (Figure 2). Transects were selected by the McMurdo Long-term Ecological Research (MCMLTER) program during the 1993-1994 summer to represent a wide gradient in physical and chemical characteristics, with roughly twice as many low coverage transects as high coverage transects. Individual descriptions of streams monitored by the MCMLTER can be found in Alger et al. (1997), McKnight et al. (1998), Stanish et al. (2011, 2012), and in depth at www.mcmlter.org. A brief description of all streams follows, along with the physical descriptions of individual transects provided in Table 1. A detailed sample history of each transect is located in Table 1 of Chapter I.

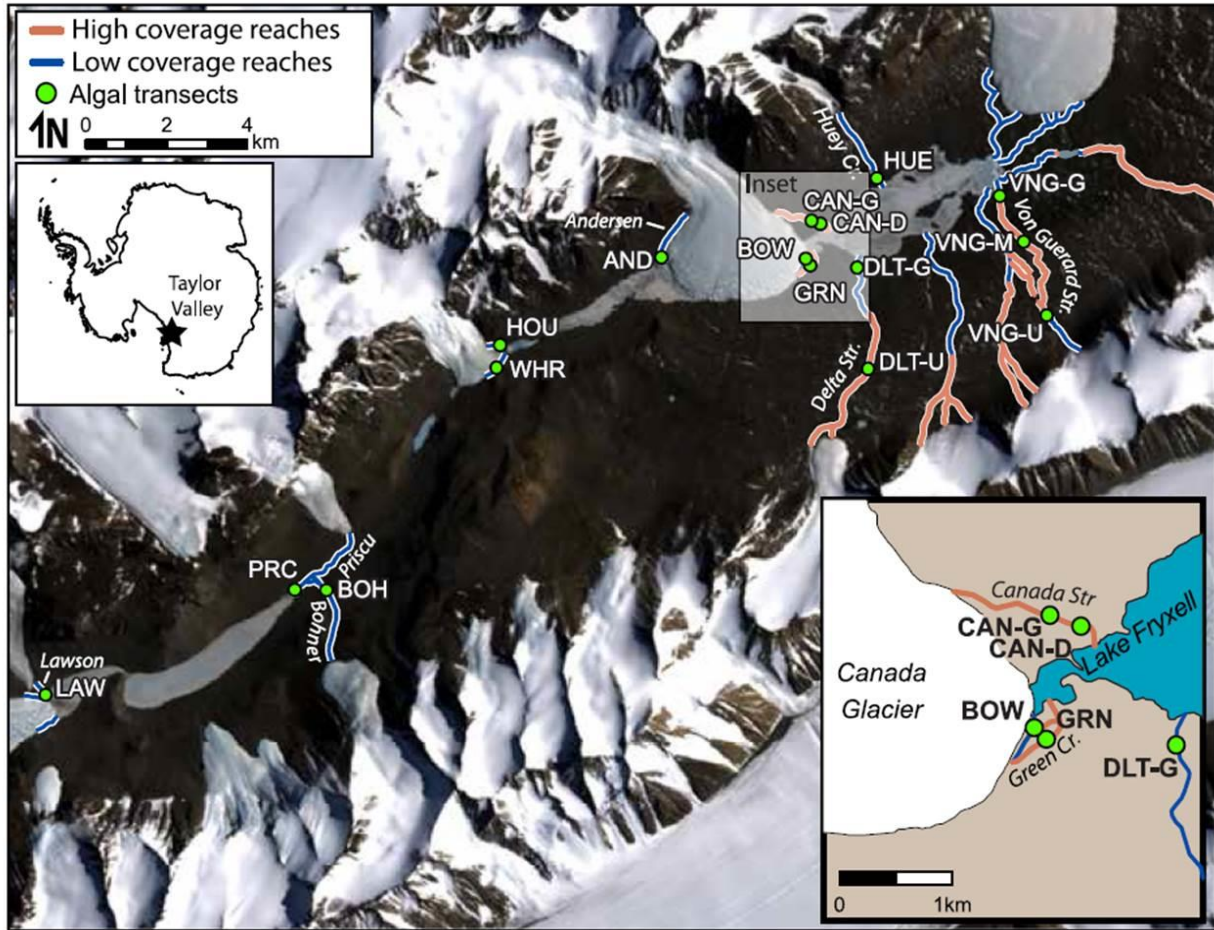


Figure 2. Map of Taylor Valley, Antarctica, with detail of the east side of Canada Glacier. Algal transects are indicated by green circles. High coverage stream reaches with abundant algal mats are colored red, and low coverage stream reaches with sparse algae are colored blue.

Lake Fryxell has the most streams of any lake basin in Taylor Valley, and has the only high coverage transects. Delta Stream is the longest stream in Taylor Valley, and drains the Howard Glacier in the Kukri Hills, while Von Guerard stream is the 2nd longest stream and drains the Von Guerard Glacier. Both of these streams have large cobble substrata at their headwaters which become finer at the outlets. Flow commences later in the season for these streams compared to shorter streams. Canada Stream drains the northeast side of Canada Glacier and has been studied extensively due to its dense microbial mats, reliable flow, and proximity to an old New Zealand camp. Green and Bowles Creeks are the shortest streams in the Fryxell basin and

Table 1. Physical characteristics of MCMLTER transects. Transects are in approximate order from west to east, and designations for coverage are taken from Table 6 in Alger et al. (1997), and are included therein as “visual algal abundance”. “Ave harshness” indicates the average harshness values with standard deviations calculated for gaged transects over the study period. For substrata type, “uneven” indicates large boulders with sand interspersed, “delta” indicates unconsolidated sandy substrata, and “pavement” indicates a stone pavement formed by freeze and thaw processes that is resistant to mobilization (McKnight et al. 1998, Alger et al. 1997).

Transect	Abbr.	Basin	Latitude (S)	Longitude (W)	Coverage	Ave. Harshness	Stream length (km)	Substrata type	Ave. pebble size (cm)	Gradient (m/m)
Lawson	LAW	Bonney	-77.72036	162.26878	Low	0.8 ± 0.8	0.3	uneven	8.44	0.07
Priscu	PRC	Bonney	-77.69637	162.53614	Low	1.4 ± 1.3	3.8	delta	3.31	0.01
Bohner	BOH	Bonney	-77.69628	162.56392	Low	-	1.2	uneven	18.00	0.25
Wharton	WHR	Hoare	-77.64465	162.74507	Low	-	1.0	delta	2.89	0.01
House	HOU	Hoare	-77.64286	162.74127	Low	1.8 ± 1.3	2.0	uneven	7.28	0.05
Andersen	AND	Hoare	-77.62281	162.90627	Low	1.6 ± 1.3	1.4	delta	8.56	0.05
Canada Gage	CAN-G	Fryxell	-77.61325	163.05322	High	1.0 ± 0.8	1.5	pavement	6.56	0.03
Canada Delta	CAN-D	Fryxell	-77.61462	163.06999	Low	-	-	uneven	7.42	0.05
Bowles	BOW	Fryxell	-77.62327	163.05776	High	-	0.9	pavement	7.61	0.03
Green	GRN	Fryxell	-77.62441	163.05936	High	2.4 ± 1.0	1.2	pavement	8.69	0.05
Delta Gage	DLT-G	Fryxell	-77.62533	163.10954	Low	3.1 ± 1.7	11.2	delta	7.63	0.05
Delta Upper	DLT-U	Fryxell	-77.65315	163.09972	High	-	-	pavement	11.52	0.10
Huey	HUE	Fryxell	-77.60231	163.12361	Low	2.9 ± 0.7	2.1	delta	6.01	0.03
Von Guerard Gage	VNG-G	Fryxell	-77.60925	163.25408	High	2.8 ± 1.4	4.9	delta	2.50	0.05
Von Guerard Middle	VNG-M	Fryxell	-77.61930	163.28836	High	-	-	pavement	11.02	0.06
Von Guerard Upper	VNG-U	Fryxell	-77.63445	163.30612	Low	-	-	uneven	15.17	0.20

drain a pond on the southeast side of Canada Glacier. Huey Creek drains a snowfield in the Asgard Range to the north, and its outlet is near Fryxell Camp. Andersen Creek drains the west side of the Canada Glacier and empties into Lake Hoare near the Lake Hoare camp. House and Wharton Creeks drain the east side of the Suess Glacier and empty into Lake Chad, which has recently merged with Lake Hoare. House Stream flows through a large boulder moraine, while Wharton is a delta. Within the Lake Bonney basin, Priscu Stream drains the Lacroix Glacier, has relatively fine substrata, and drains into the east lobe of Lake Bonney. Bohner Stream has a high gradient with a boulder substratum and drains the Sollas Glacier to the south, eventually merging with Priscu Stream. Lawson Stream drains the Rhone Glacier, and also has a steep gradient, boulder substratum, and empties into Lake Bonney's west lobe.

Microbial Mat Collection and Analyses

Microbial mats were sampled opportunistically along transects in early to mid-January beginning in the 1993-1994 season. The last flow season for this dataset includes samples from 2012-2013. Mat type was identified as green, orange, red, or black, and the presence or absence of each mat type was noted during each site visit regardless of whether biomass was sampled. In 1993-1994, the abundance of algal mats in the 12 streams was visually characterized as low (<50% cover) or high (>50% cover), and changes, if any, were noted in subsequent years (Table 1, Alger et al. 1997). The substratum was characterized by estimating the average pebble size for each transect as outlined by Wolman (1954). Mat samples were collected using a brass cork borer (1.7 cm diameter) for each of chlorophyll-a (Chl-a) and ash-free dry mass (AFDM) analysis and placed into Whirlpack® bags with stream water. Up to five replicates were taken for each analyte. Mat

samples were then mapped at each transect with a Leica® Total Station Theodolite (Leica Geosystems), which also provided an estimate of the reach gradient (Alger et al. 1997).

In the laboratory, samples were de-watered on pre-combusted Whatman® GF/C filters, wrapped in aluminum foil, and stored in the dark at -20°C. Prior to the year 2000, Chl-a samples were extracted in buffered acetone and analyzed spectrophotometrically using the trichromatic method (Strickland and Parson 1972). After 2000, Chl-a was extracted in buffered acetone and analyzed using a Turner Designs 10-AU field fluorometer (Welschmeyer 1994). Both methods have been shown to produce comparable Chl-a results (Lorenzen and Jeffrey 1980). For AFDM analysis, samples were dried at 100°C for 24 h, weighed, burned at 450°C for 4 h and re-weighed, and then re-wetted and dried to determine mass loss due to hydration of sediments (Steinman et al. 1996). Both Chl-a and AFDM analyses were performed at Crary Laboratory in McMurdo Station. An autotrophic index (AI) was calculated as the ratio of Chl-a to AFDM. Biomass data were averaged to provide one number for each mat type for each transect for each season.

Hydrologic Indices and Water Chemistry Data Collection

Continuous flow measurements for Taylor Valley streams were initiated in 1990 in collaboration with the U.S. Geological Survey. Stream gages are located near the stream outlets to the lakes (except Bohner, Bowles, and Wharton, which were not gaged), and stage measurements are taken at 15 minute intervals by pressure transducers from which discharge is calculated. From these data, we designated “season length” as the number of days from the first to the last day of flow for a given stream for a particular season. The “average daily discharge” and the “total discharge” were calculated for each stream for each season based on flow between December 1st

and January 31st, which captures the bulk of the flow for most streams and excludes the intermittent low flows before and after this time period. To quantify the potential for streambed desiccation within a season, we counted the number of days without flow within this timeframe and called these “zero flow days”. The number of high flow days for a given stream for a season, or “flood days”, was calculated as a day with an average daily discharge of at least three times the 10-year average for that given stream, with the average 10-year daily discharge calculated from the first ten seasons of flow data (1993-1994 through 2002-2003).

We used the above hydrologic metrics to calculate a harshness index, H_s (Equation 1) building upon the harshness rankings calculated by Esposito et al. (2006), which was modified from the index in Fritz and Dodds (2005) developed for temperate grasslands. The resulting values are a way to integrate, quantify and compare hydrologic extremes of high and low flows observed across different sites. The H_s was standardized for comparison across all streams and seasons by using one stream as a baseline for the index. Canada Stream was chosen because it has the most complete stream flow record and the most reliable annual flow. Harshness was defined as:

$$H_s = [(F_s / \overline{F_C}) + (| (M_s - \overline{M_s}) / \overline{M_s} |) + (Z_s / \overline{Z_C})] / 3$$

Where H_s is the harshness index of stream S for season Y , F_s is the number of flood events for stream S in season Y , and $\overline{F_C}$ is the 10-year average number of flood events for Canada Stream. The second term designates the deviation from the historical mean (“historic deviation”), where M_s is the mean daily discharge for stream S during season Y , and $\overline{M_s}$ is the 10 year mean daily discharge for stream S . The third term, Z_s , indicates “zero flow days” as described above, and is

the number of days without flow in season Y for stream S , and $\overline{Z_C}$ is the 10-year average number of zero days for Canada Stream.

Statistical Analyses

All mats types were not found in all streams, and even where historically present, mats were not found in all seasons. Additionally, in some seasons, mats did not receive flow and remained inactive, and in some seasons (for example, the flood year) logistic, technical, and safety concerns prevented sampling. The temporal scale at which hydrologic data were collected also varied. Discharge was measured every season with the exception of three algal transects (Wharton, Bohner, and Bowles) that are located on ungaged streams, and four other transect sites that are found several km above the gaging stations (Delta Upper, Von Guerard Upper, Von Guerard Middle, and Canada Delta). For these upstream sites, discharge likely differs from what was measured at the downstream gage due to evaporative losses or the addition of a downstream tributary. Less frequently, a stream gage failed due to sedimentation or streambed mobilization, as in Priscu Stream and Huey Creek. Therefore, the number of observations for each stream differed considerably, and consequently had different levels of variability. As a result of these challenges, as well as the existence of temporal autocorrelation for biomass data resulting from the perennial nature of the microbial mats, a direct comparison of biomass data to environmental variables (that is, through regression) was not possible. This is not only because a direct comparison would violate statistical assumptions, but also because the resulting sample size of paired variables would be too small to sufficiently explain observed variation despite 20 years of data.

To overcome these challenges, we modeled biomass and hydrologic indices separately as a function of time using generalized additive mixed models (gamm) because they allow for the use of variance functions and correlation structures. Prior to analysis of the 20-year dataset, we conducted an exploratory data analysis (Zuur et al. 2010) for biomass and flow data to assess normality, potential outliers, heteroscedasticity, and temporal independence. All variables that were not normally distributed were square-root or log-transformed to satisfy the assumption of normality. In order to avoid violating homogeneity of variance assumptions, categorical variables were allowed to vary independently by employing variance structures as random effects, using the R function “varIdent” (Zuur et al. 2009). Additionally, we accounted for temporally autocorrelated transect data using an auto-regressive moving average serial correlation structure (ARMA) that models each date as a function of previous dates (Zuur et al. 2009) if necessary. Stream of origin and/or season were included as random effects if it improved model fit, as evaluated by assessing the model residuals.

We chose to model flood days, zero flow days, season length, historic deviation, and total discharge as hydrologic indices to compare with biomass variables, as calculated above. Harshness did not produce a significant smoothed model, and average daily discharge was collinear with total discharge ($PCC = 0.98$). To test how streams of different geomorphologies respond to flow variables over time, biomass data were split by high and low coverage transects as reported in Table 6 of Alger et al. (1997), and we modeled the changes in Chl-a, AFDM, and AI through time for each microbial mat type. Models were additionally created and analyzed for all combined transects for comparison, and the results are included as Figure A3-A4 and Table A2-A3 in the Supplemental Material. We then applied Gaussian smoothers to each of these

models using the “mgcv” R package (Wood 2014), which resulted in the 20-year smoothed trend for a particular variable.

Once smoothed lines were created, it was possible to determine the strength of individual relationships between hydrologic and biomass variables by calculating Pearson correlation coefficients (PCC) between the smoothed lines (utilizing 20 time points corresponding to each of the 20 years) using the “Hmisc” R package (Harrell and Dupont 2014). We synthesized these individual results by evaluating the average direction and magnitude of individual hydrologic variables on mat biomass. To assess if a particular hydrologic variable had an overall positive or negative relationship with mat biomass in the MDVs, we averaged the PCCs generated between a given hydrologic index and the combined Chl-a and AFDM of the three mat types. To assess the overall magnitude (size of effect) a hydrologic index had on mat biomass, we took the average absolute value of the PCCs generated between the given hydrologic index and the Chl-a and AFDM of the three mat types. To evaluate which mat type had the greatest overall relationships with the modeled hydrologic indices, we averaged the absolute values of PCCs calculated between the biomass of a given mat type and all hydrologic variables. To visualize how these associations differ with stream geomorphology, these analyses were conducted for high coverage transects, low coverage transects, and all transects combined (see Supplemental Materials).

To test which combination of hydrologic variables best predicts mat AFDM and Chl-a from high, and low coverage transects, we extracted the output from each gamm model ($n = 20$), and from this new data matrix created linear models (Zuur et al. 2007). Candidate models compared for each mat and biomass type included a global model, which included all explanatory variables, and a “null” model to serve as background. After candidate models were

created, they were ranked using Akaike's Information Criterion (AIC) corrected for small sample sizes (AIC_c), where the lowest AIC_c value indicates the highest rank (Burnham and Anderson 2002). We additionally calculated the ΔAIC_c (the difference between individual AIC_c values and the lowest AIC_c value), the weight (probability that an individual model is the best approximating model for the data), the log-likelihood, and adjusted R-squared of each model. AIC_c penalizes over-fitting data with independent variables, which can happen in multiple regression models. All statistical analyses were performed using the R console, version 2.13.0 (R Development Core Team 2014).

RESULTS

Comparison of the Diverse Stream Sites in the MDV

Fryxell basin streams had greater harshness values on average than streams in the Hoare or Bonney basins (Table 1). Von Guerard, Delta, and Huey exhibited the greatest average harshness, presumably due to their length which predisposes them to more instances of desiccation and freeze-up. The most consistent microbial mat diversity was observed in high coverage streams, which had greater average numbers of mat types over the 20-year monitoring period (Figure 3A). The Fryxell basin exhibited the greatest average number of microbial mat types over the 20-year period, followed by Hoare and Bonney basins. The Canada Stream gage transect maintained the greatest mat type diversity over time, in contrast with Lawson and Priscu stream transects which had less than one mat type present on average over the 20-year period. Orange mats were the most common microbial mat encountered across sites and were found in all 16 transects (Figure 3B). Green mats were the second most commonly encountered microbial mat, and were found in all streams except for Priscu, though their presence is more variable from

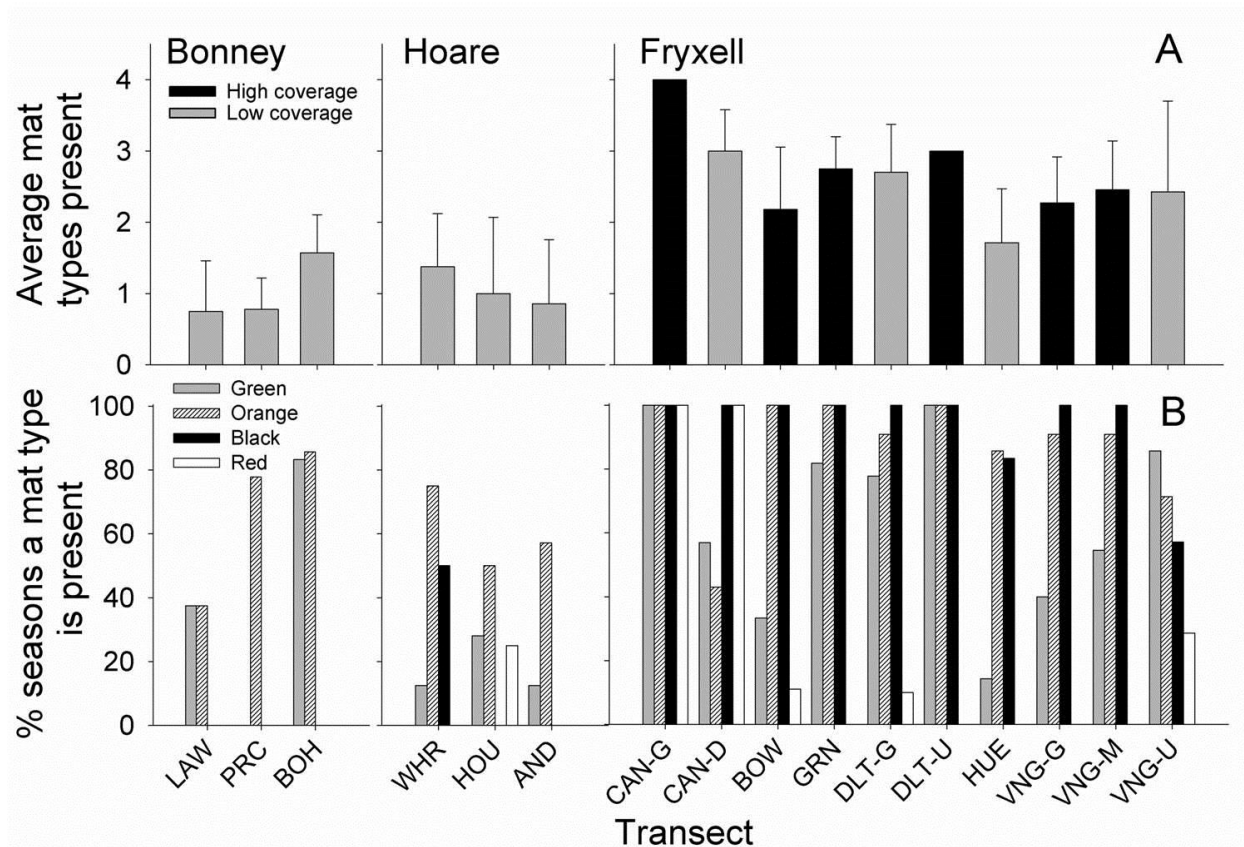


Figure 3. (A) Average number of observed mat types per season. High coverage transects are indicated by black bars and low coverage transects by grey bars. Error bars indicate standard deviation, and where absent falls within the bar. (B) The percent of seasons where a particular mat type was observed. All data are separated by stream transect and lake basin, and observations range from n = 6 to 14 (see Table 1 in Chapter I).

year to year in comparison with orange mats. Black mats were less widely distributed throughout Taylor Valley, and outside of the Fryxell basin were only observed in the Wharton Creek transect. However, when present, black mats were less likely than other mat types to disappear from transects from one season to the next. Of the 11 transects where black mats were found, nine transects had black mats present on 100% of seasons visited. Red mats had the most narrow distribution, and were only infrequently present in five transects, with the exception of Canada Gage and Canada Delta, where they were present on every season visit.

Trends in Hydrology and Microbial Biomass

Canada Stream, which has the most consistent streamflow of any stream in Taylor Valley, showed a period of low flow from 1993-1994 until interrupted by the flood year in 2001-2002. Greater than average flows followed until the end of the study period, with high flows occurring again in 2008-2009 and 2010-2011 (Figure 4). The smoothed trend line for total discharge reflects measurements for Canada Stream with a noticeable peak in 2002, and elevated discharges in the last 10-year period (Figure 4). The smoothed trend for season length was non-linear and produced peaks in 1999, 2005, and 2011 (Figure 4). Flood days increased after 2001-2002 (Figure 4), and zero flow days decreased throughout the last 10-year period (Figure 4). Lastly, the trend for the historic deviation model produced peaks around 2002 and 2011 (Figure 4). All gamm models for hydrologic indices were highly significant (Table 2).

High coverage streams had greater standing biomass than low coverage streams (Figure 5), and mat biomass in general was stable or declined through the low flow summers of the first decade until the high flow year. For most streams and mat types, AFDM and Chl-a was about half the original value in 2001 than was measured in 1994. Similarly, biomass from nearly all streams was lower the year after the 2001-2002 flood than the preceding year, with the exception of Von Guerard Stream, which had little or no flow recorded in the 2000-2001 season. After 2003, mat biomass from streams increased over the second decade to levels equal to or greater than that observed in the early 1990's. Green mats were also reported in Wharton Stream for the first and only time the year after the flood, and were overall more frequently encountered across streams in the last 10 years than the 10 before. All three mats types exhibit a peak in AI after the flood year, suggesting greater concentrations of Chl-a relative to AFDM in these higher flowing summers (Figure 5).

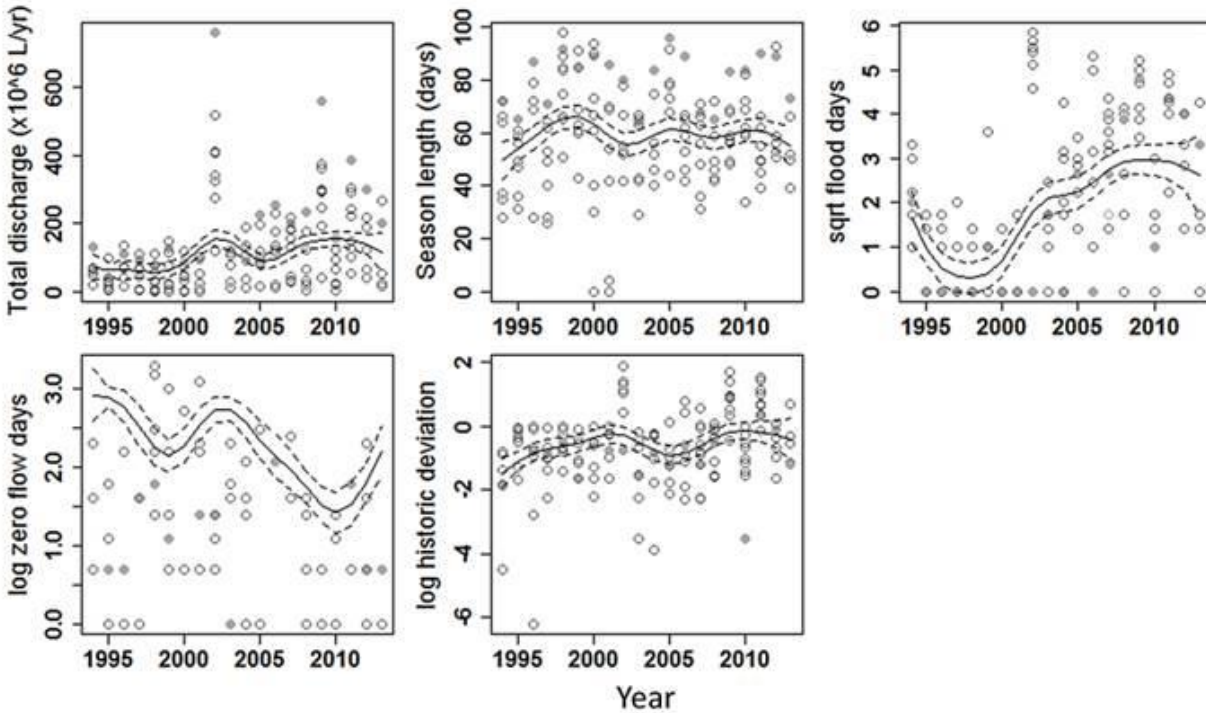


Figure 4. Scatterplots showing total discharge, season length, flood days, zero flow days, and historic deviation as outlined in the Methods section for gaged streams from 1993-1994 to 2012-2013. Canada stream is plotted as a reference in all figures with grey filled circles. The smoothed line is superimposed, and represents the modeled best-fit trend for the entire dataset, and dotted lines indicate 95% confidence intervals.

Table 2. Smoothed model statistical output for hydrologic indices including the model estimate, adjusted R^2 , model p-value, parameter F-statistic, and parameter p-value.

Parameter coefficients for hydrologic indices						
parameter	estimate	t-value	p-value	adj R^2	F-value	p-value
flood days	1.82	13.03	<0.01	0.31	28.31	<0.01
zero flow days	2.24	12.74	<0.01	0.93	16.35	<0.01
season length	59.40	15.05	<0.01	0.83	2.63	0.02
historic deviation	-0.57	-5.55	<0.01	0.11	4.95	<0.01
total discharge	1.09E+08	6.05	<0.01	-0.16	10.69	<0.01

All biomass models were highly significant, with the exception of high coverage green mat AI and low coverage green mat Chl-a (Table 3), and should be interpreted with caution. Smoothed trends differed in their direction and magnitude between high and low coverage transects (Figure 5). For example, green mat AFDM in low coverage transects generally decreased from the beginning of the 20-year period, while the same value in high coverage transects increased.

Table 3. Smoothed model statistical output for biomass variables from high and low coverage transects. Model estimate, adjusted R^2 , model p-value, parameter F-statistics, and parameter p-values are included. Shaded boxes are those models with p-values greater than 0.05.

Parameter coefficients for mat biomass					High coverage		Low coverage	
parameter	estimate	t-value	p-value	adj R^2	F-value	p-value	F-value	p-value
G_AFDM	0.97	4.28	<0.01	0.09	4.95	0.01	3.21	0.04
G_Ch1-a	0.66	4.01	<0.01	-0.12	11.16	<0.01	1.49	0.23
G_AI	1.18	14.33	<0.01	0.32	0.08	0.81	6.53	<0.01
O_AFDM	2.14	8.21	<0.01	0.51	5.40	<0.01	7.05	<0.01
O_Ch1-a	1.94	8.60	<0.01	0.64	3.96	0.01	10.08	<0.01
O_AI	1.01	22.51	<0.01	0.97	9.26	<0.01	18.96	<0.01
B_AFDM	4.60	46.37	<0.01	1.00	41.38	<0.01	48.50	<0.01
B_Ch1-a	2.93	14.46	<0.01	0.99	14.12	<0.01	6.64	<0.01
B_AI	0.87	23.73	<0.01	0.46	7.26	<0.01	4.30	<0.01

Correlation between Microbial Biomass and Hydrology

To test how the biomass of different mat types is related to high and low flows, we compared the trends in hydrologic variables with the trends in high and low coverage mat biomass. In high coverage transects, green mat biomass was highly correlated with many hydrologic variables (Figure 6). Total discharge was positively correlated with green mat AFDM (PCC = 0.54) and Chl-a (PCC = 0.64). Historic deviation was positively related to green mat AFDM (PCC = 0.43) and Chl-a (0.53) (Figure 6), along with flood days (AFDM = 0.77, Chl-a = 0.82). Conversely, zero flow days were negatively correlated with green mat AFDM (PCC = 0.71) and Chl-a (PCC = 0.75). Orange and black mat biomass had relatively weaker correlations with hydrologic

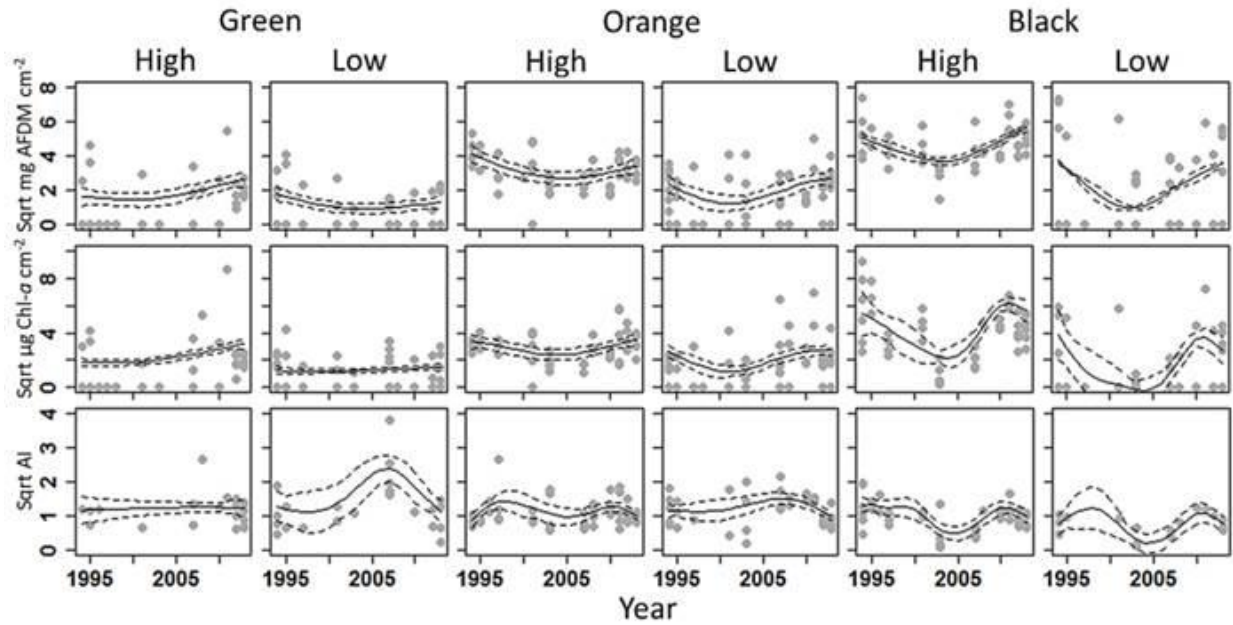


Figure 5. Long-term trends in ash-free dry mass (AFDM), chlorophyll-a (Chl-a), and the autotrophic index (AI = Chl-a:AFDM) created for green, orange, and black mat types modeled separately by high and low coverage transects. Data are square-root transformed, and points are averaged values for each transect for each season. The corresponding smoothed trend lines are superimposed on each figure, and dotted lines indicate 95% confidence intervals.

variables. High coverage orange mats were most strongly correlated with total discharge, which was negatively correlated with both orange AFDM (PCC = 0.55) and Chl-a (PCC = 0.20), and season length, which was also negatively correlated with biomass (AFDM PCC = 40, Chla PCC = 30). Orange AFDM was also negatively related to flood days (PCC = 0.43), historic deviation (PCC = 0.50), and positively related to zero flow days (PCC = 0.36, Figure 6). Correlations between high coverage black mats and hydrology were poor, and the best relationship was between zero flow days and Chl-a (PCC = 0.46), which was negative (Figure 6).

Relationships between hydrology and biomass were considerably different for low coverage transects. While correlations with green mat Chl-a was largely unchanged between high and low coverage transects, relationships between AFDM and hydrologic variables were

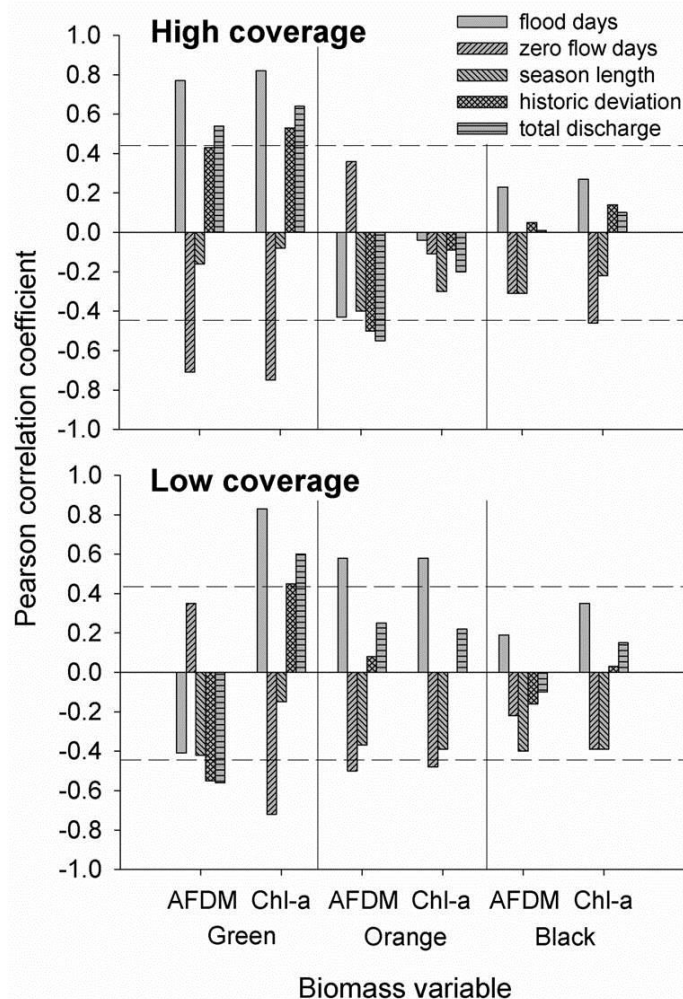


Figure 6. Bar graphs of Pearson correlation coefficients showing the strength and direction of correlations between hydrologic indices and mat biomass for high (top) and low (bottom) coverage transects. PCC's (y-axis) were calculated by comparing ash-free dry mass (AFDM) and chlorophyll-a (Chl-a) of different mat types (x-axis) with hydrologic indices (in legend). The sign of the coefficient indicates whether the relationship is positive or negative, and dotted horizontal lines roughly indicate significance of correlations at $p = 0.05$.

almost opposite in low coverage transects (Figure 6). Green AFDM was reduced by increased flood days (PCC = 0.41), total discharge (PCC = 0.56), and historic deviation (PCC = 0.55). Green AFDM also increased with zero

flow days (PCC = 0.35). Orange mats displayed a strong positive correlation with flood days in terms of both AFDM (PCC = 0.58) and Chl-a (PCC = 0.58). Conversely, zero flow days were negatively related to orange mat AFDM (PCC = 0.50) and Chl-a (PCC = 0.48). Both of these comparisons are opposite that observed in high coverage transects. Season length was negatively correlated with orange mat AFDM (PCC = 0.37) and Chl-a (PCC = 0.39), which was also observed in high coverage transects. Correlations were not substantially changed for black mat biomass, and the direction of the relationships between all variables remained the same as in high coverage transects with the exception of historic deviation and total discharge, which had negative relationships (Figure 6).

By averaging the PCCs across all mat types, we were able to visualize the general relationships of the hydrologic parameters with mat biomass in MDV streams (Figure 7). Zero flow days and season length were both negatively related to biomass for all transects, while the high-flow parameter, flood days, was generally associated with increases in biomass. Historic deviation and total discharge were more ambiguous in their relationships with mat biomass, though averages were mostly positive (Figure 7A). When the magnitude of correlations was examined by calculating the mean of PCC absolute values (Figure 7B), flood days and zero flow days (the most extreme hydrologic conditions) produced the strongest correlations for both high and low coverage transects. Total discharge and historic deviation were more influential for high coverage streams, while season length was more influential on low coverage streams (Figure 7B). Lastly, we evaluated the importance of hydrologic variables to individual mat types by averaging the absolute values of PCCs calculated for each mat type. Green mats had the largest values, followed by orange and then black mats (Figure 7C). For green mats, the average correlation values were greatest for all transects combined, followed by high and then low coverage transects. By contrast, separating transects into high and low coverage improved relationships for orange and black mats, and the average PCCs further increased from high coverage to low coverage streams, respectively (Figure 7C).

Candidate linear models were compared with AIC_c to investigate which combinations of hydrologic variables best predict mat biomass from high and low coverage transects. The best models for green mat AFDM and Chl-a from high coverage streams included flood days, season length, total discharge, historic deviation, and garnered 84% and 88% of the weight, respectively. In low coverage streams, green Chl-a shared the most parsimonious model as high coverage green mats, but low coverage green AFDM incorporated zero flow days instead of historic

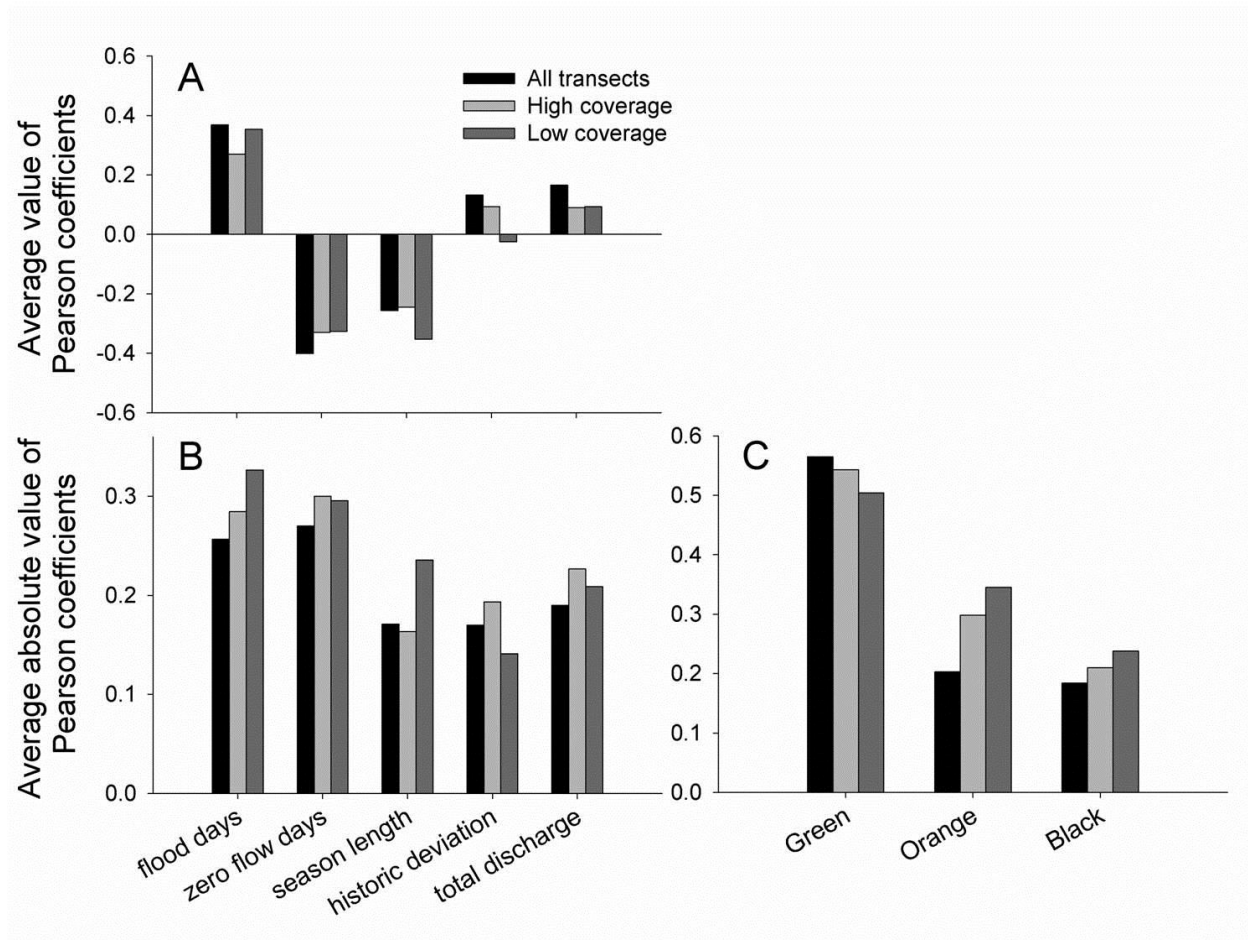


Figure 7. The overall influence of hydrologic parameters on mat biomass (AFDM and Chl-a) using averaged Pearson correlation coefficients (PCCs). Panel (A) shows the positive or negative influence of a given hydrologic parameter on all mat types by averaging PCCs separately by high coverage, low coverage, and all combined transects, (B) the magnitude of influence of each hydrologic variable on all mat types using absolute values of the average PCCs, and (C) the relative importance of all measured hydrologic variables in predicting biomass for each mat type, where bars represent the average PCCs of all AFDM and Chl-a comparisons made with hydrologic parameters for a particular mat type. Notice the change in scale between the y-axes of panels B and C. See Supplemental Materials for information concerning combined transect models.

deviation (Table 4). Low coverage orange mat AFDM and Chl-a were best explained by season length, total discharge, and zero flow days, capturing 69% and 78% of the weight. High coverage orange mat models included these three variables as well, but the best AFDM model also included floods and Chl-a included historic deviation (Table 4). Black AFDM shared the best

model between high and low coverage streams, with total discharge, historic deviation, zero days, and season days as variables, having 81% and 50% of the weight respectively. The best models for black mat Chl-a both included flood days, season length, and zero flow days, but differed in that high coverage transects also included total discharge, and low coverage included the historic deviation (Table 4).

Although season length and total discharge were not always highly correlated with mat biomass through PCC's, they were the only two variables included in all of the highest ranking models. The exception to this is black mat Chl-a from low coverage streams, which lacks total discharge. Additionally, the best models for orange and black mat AFDM and Chl-a all included zero flow days, although this was not included for either of the best models explaining green mat biomass from high coverage transects.

DISCUSSION

In this analysis, we found green mats, which form streamers elevated from the streambed, to have the greatest correlations with hydrologic variables. These were followed by orange mats which grow on the bottom of the stream channel, and black mats, which grow outside the stream at the banks and margins. The strength of these correlations was similar between high and low coverage streams, but the direction of these individual effects (positive or negative) differed considerably. Lastly, when models incorporating multiple variables explaining biomass of mat types were ranked with AICc, the best explanatory models were different for the three mat types, but also between high and low coverage transects. Collectively, these results suggest that previously identified sources of heterogeneity, such as geomorphologic characteristics (Cardinale et al. 2002, Fuller et al. 2011), taxonomic identity (Stevenson 1996, Biggs et al. 1998, Hart et al.

Table 4. AICc output and adjusted R² values for linear models describing green, orange, and black mat AFDM and Chl-a for high and low coverage models. Shown are only those models with weights greater than or equal to 10% (Royall 1997). AIC indicates Akaike's Information Criterion, k indicates the number of parameters (including intercept and error terms), $\Delta AICc$ is the difference between the AICc value and the lowest AICc value, AICcWt is the relative likelihood that the model is the best approximating model, Cum.Wt is the cumulative weight, and LL is log likelihood. Variable abbreviations are as follows: "floods" = flood days, "season" = season length, "zeros" = zero flow days, "historic" = historic deviation, and "total_dis" = total discharge.

Models	k	AICc	$\Delta AICc$	AICcWt	Cum.Wt	LL	adj R ²
High coverage							
G_AFDM							
floods + season + total_dis + historic	6	-9.09	0	0.84	0.84	13.78	0.92
floods + season + zeros + total_dis + historic	7	-5.43	3.66	0.14	0.98	14.38	0.91
G_Chla							
floods + season + total_dis + historic	6	-9.24	0	0.88	0.88	13.85	0.92
floods + season + zeros + total_dis + historic	7	-4.95	4.29	0.10	0.99	14.14	0.91
O_AFDM							
floods + season + zeros + total_dis	6	-3.06	0	0.70	0.70	10.76	0.84
floods + season + zeros + historic	6	-0.8	2.26	0.22	0.92	9.63	0.83
O_Chla							
total_dis + historic + zeros + season	6	6.53	0	0.73	0.73	5.96	0.69
B_AFDM							
total_dis + historic + zeros + season	6	23.07	0	0.81	0.81	-2.30	0.72
B_Chla							
floods + season + zeros + total_dis	6	51.91	0	0.37	0.37	-16.72	0.78
floods + season + zeros	5	52.15	0.24	0.33	0.70	-18.93	0.75
floods + season + zeros + historic	6	53.77	1.86	0.15	0.85	-17.65	0.76
total_dis + historic + zeros + season	6	54.58	2.67	0.10	0.95	-18.06	0.75
Low Coverage							
G_AFDM							
floods + season + zeros + total_dis	6	-26.42	0	0.59	0.59	22.44	0.86
floods + season + zeros + historic	6	-25.29	1.13	0.34	0.93	21.88	0.85
G_Chla							
floods + season + total_dis + historic	6	-73.52	0	0.91	0.91	45.99	0.92
O_AFDM							
season + total_dis + zeros	5	5.53	0	0.69	0.69	4.38	0.82
total_dis + historic + zeros + season	6	8.32	2.78	0.17	0.87	5.07	0.82
O_Chla							
season + total_dis + zeros	5	4.52	0	0.78	0.78	4.88	0.87
total_dis + historic + zeros + season	6	8.56	4.05	0.1	0.88	4.95	0.86
floods + season + zeros + total_dis	6	8.67	4.15	0.1	0.98	4.9	0.86
B_AFDM							
total_dis + historic + zeros + season	6	34.17	0	0.50	0.50	-7.86	0.79
floods + season + zeros + total_dis	6	35.31	1.14	0.28	0.78	-8.43	0.78
season + total_dis + zeros	5	36.65	2.47	0.15	0.93	-11.18	0.73
B_Chla							
floods + season + zeros + historic	6	50.81	0	0.39	0.39	-16.17	0.82
floods + season + zeros + total_dis	6	50.94	0.14	0.36	0.76	-16.24	0.82
floods + season + zeros	5	52.37	1.57	0.18	0.93	-19.04	0.77

2013), and multiple hydrologic indices (Clausen and Biggs 2000), should be integrated to best predict primary production dynamics in stream ecosystems. This information is not only critical to evaluating how a changing hydrologic regime will impact MDV microbial ecosystems in the future, but also other ephemeral (Dodds et al. 2004), desert (Grimm and Fisher 1989), and arctic (Huryn et al. 2005, Parker and Huryn 2011) streams. Finally, the application of these results can be useful in predicting the spread of and ultimately managing nuisance mat-forming algae such as *Didymosphenia geminata* (Cullis et al. 2012).

Proposed Mechanisms for Differences in Mat-Type Response

Differences between mat types

The decrease in biomass for all microbial mat types during the first decade, and subsequent increase in the second, parallels other MDV biological compartments. Nematode populations decreased from 1993 to 2005 (Barrett et al. 2008), and lake primary production decreased 6-9% annually over roughly the same time period (Doran et al. 2002). Nonetheless, individual mat types showed distinct relationships with flow variables, likely because they utilize different habitats within the stream. Orange mats are found where continuous flow occurs, including on sand, over stable stone pavements, or in the interstices of large immobile rocks both within and outside the channel. Green and black mats consistently occur in distinct habitats regardless of high or low coverage, and are found attached to large stones and over the hyporheic zone at the stream margin, respectively.

Green mats had the highest correlations with hydrologic variables of all three mat types, which may indicate the importance of continuous flow to the growth of these communities. Previous investigations have found chlorophytes to dominate the turbulent areas of Maritime

Antarctic streams where cyanobacterial mats were excluded (Hawes and Brazier 1991, Rochera et al. 2013), indicating either superior tolerance or possible preference for higher flows, which is in line with our observations (Figure 1, X₂). However, sloughing is still likely to be an important regulatory mechanism (Hawes 1989), especially in low coverage streams where sediment loads may be higher and side channels do not provide suitable habitat. In high coverage streams, greater occurrences of zero flow days were generally associated with a reduction in green mat biomass (Figure 1, X₆), and their elevation off the streambed may make them more susceptible to desiccation during low flows.

The relationship between hydrology and orange mats is of particular importance to organic transport in MDV streams (Cullis et al. 2014), since orange mats typically have the greatest standing biomasses across sites (McKnight and Tate 1997, McKnight et al. 1998), though black mats may be comparable in some streams. Orange mats are more prone to the added stresses of recurring and variable diel peaks in flow because of their location within the stream due to sediment loads and dislodged cobbles (Figure 1, X₁; Vincent and Howard-Williams 1986). Additionally, stronger negative relationships between orange mat biomass and zero flow days may occur because orange mats recover more slowly from desiccation than black mats (Hawes et al. 1992).

While loosely attached black mats may be vulnerable to scour under high flow conditions (Dodds et al. 1995), we hypothesized that their position along the stream margins would make them less likely to be scoured by moderate discharges. Additionally, their location over the wetted hyporheic zone and quick recovery from drying should make them more tolerant of desiccation (Hawes et al. 1992). In this analysis, we found our hypothesis was supported in that black mat biomass was less well correlated with hydrologic variables compared with other mat

types. While black mats may certainly be scoured under highly elevated discharges such as the 2001-2002 flood year, relationships between black mat biomass and high flow indices such as total discharge and flood days were generally positive (though non-significant), indicating that these mats may instead be stimulated by the additional moisture and nutrients that are made available.

Differences between habitats

We predicted that physical characteristics of streams are likely to lead to differences in the response of mats to flow. Mat coverage is enhanced in stone pavement reaches presumably because flow is distributed across a wide channel under low flow conditions, and orange (and to a lesser extent black) mat coverage has been shown to be a function of the wetted perimeter of some streams (Howard-Williams et al. 1989). In low coverage reaches, similar discharges may often be observed in narrower channels with deltaic or talus substrata, and may lead to increased instances of scour. Therefore, it is in the marginal habitat and backwaters (side-arms and washes, Howard-Williams et al. 1986) of low coverage streams that colonization of cyanobacterial mats generally takes place, where scour by fine particles and dislodging of substrata may be less likely (Vincent and Howard-Williams 1986, Howard-Williams and Hawes 2007, Rochera et al. 2013).

The direction and magnitude of correlations with hydrologic indices were altered substantially for green and orange mats when separated by high and low coverage streams. The positive relationship between greater flood days and orange mat biomass in low coverage streams may indicate the opening of marginal habitats (Figure 1, X₄), and these streams may even require a threshold discharge for mats to be present. Similarly, the reduction of orange mat biomass with greater zero flow days may indicate loss of suitable habitat at stream margins

(Figure 1, X₇). Unlike orange mats, green mats are generally unable to colonize the marginal areas and instead may be scoured, which may explain the negative association between green mat AFDM and elevated discharges in low coverage streams (Figure 1, X₃). Black mats were also negatively related to low flows in high coverage streams, which may indicate a constricted wetted area (Figure 1, X₅; Howard-Williams et al. 1989).

From maps generated from surveying at the time samples were taken over the study period, orange and black mats from many low coverage streams (e.g. Bohner, Delta Gage, Wharton) are found in the same backwater areas year after year characterized by coarse, sandy substrata away from the thalweg, while high coverage streams are routinely sampled across the full length of streambed (Alger et al. 1997, McKnight et al. 1998). Transects at the mouth of longer streams (e.g. Delta Gage) may experience longer periods of desiccation than other streams, and greater than average flow seasons may not only be necessary for hydration, but may spur periods of exceptional productivity. On the other hand, in regularly flowing, high coverage streams such as Canada Stream and Green Creek, greater flows may increase the chance that material will be scoured away since there is inherently more mat material in the channel. Conversely, zero flow days may indicate the prevention of scour rather than inhibition of growth in these streams. These fundamental differences in geomorphology may then partially explain differences in the observed relationships between mat biomass and hydrology in streams of different coverages.

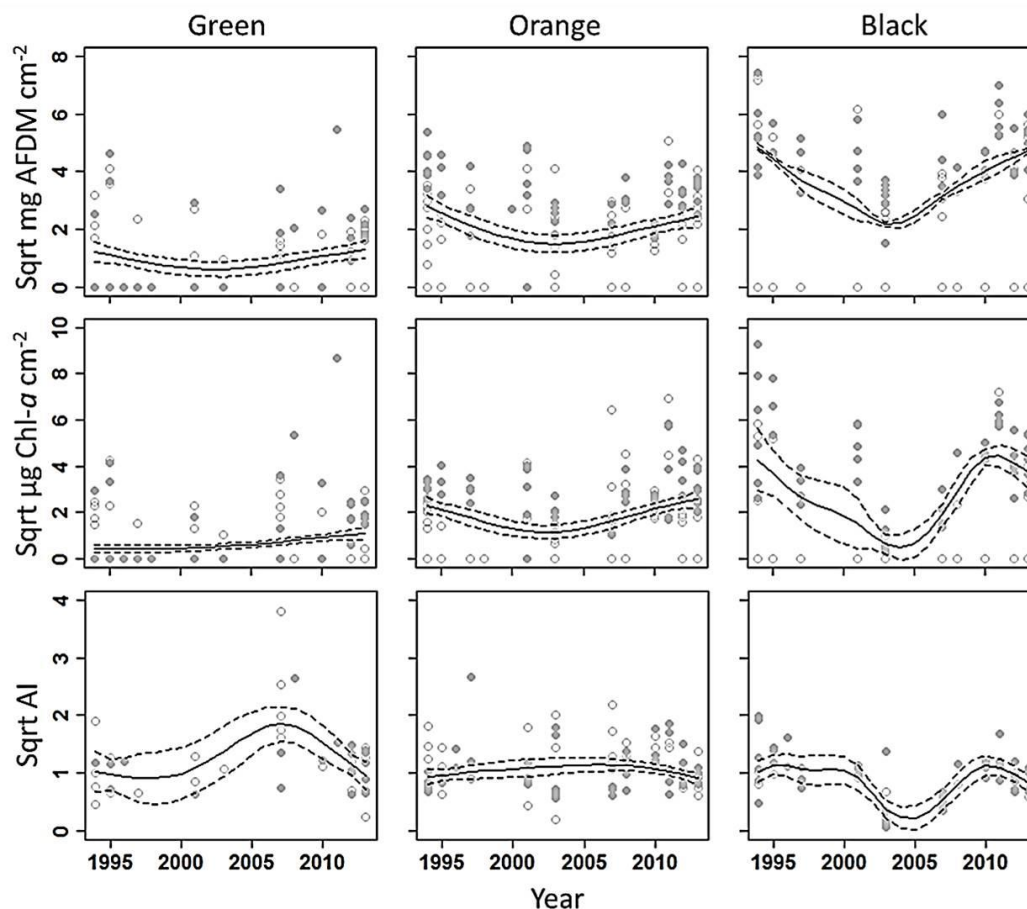
Conclusions

Future forecasted alterations in streamflow will affect mat biomass in MDV streams, though the response will ultimately depend on the mat type and stream channel geomorphology. Biomass in

high coverage streams may be maintained or decrease, while in low coverage streams mats may be stimulated. These fluctuations will undoubtedly have implications for within-stream ecosystems and those at the outlets, both in terms of the mobilization and transport of organic material, as well as biogeochemical cycling. This study provides a model for investigating the dynamics and resilience of aquatic habitats in hydrologically controlled systems worldwide, and may help inform predictive models to understand the effects of local and global-scale changes. Moreover, these observed trends are inextricably linked with historic processes that shaped stream morphology, as well as ecologic processes, such as the habitat preferences and life histories of cyanobacteria and chlorophytes.

ACKNOWLEDGEMENTS

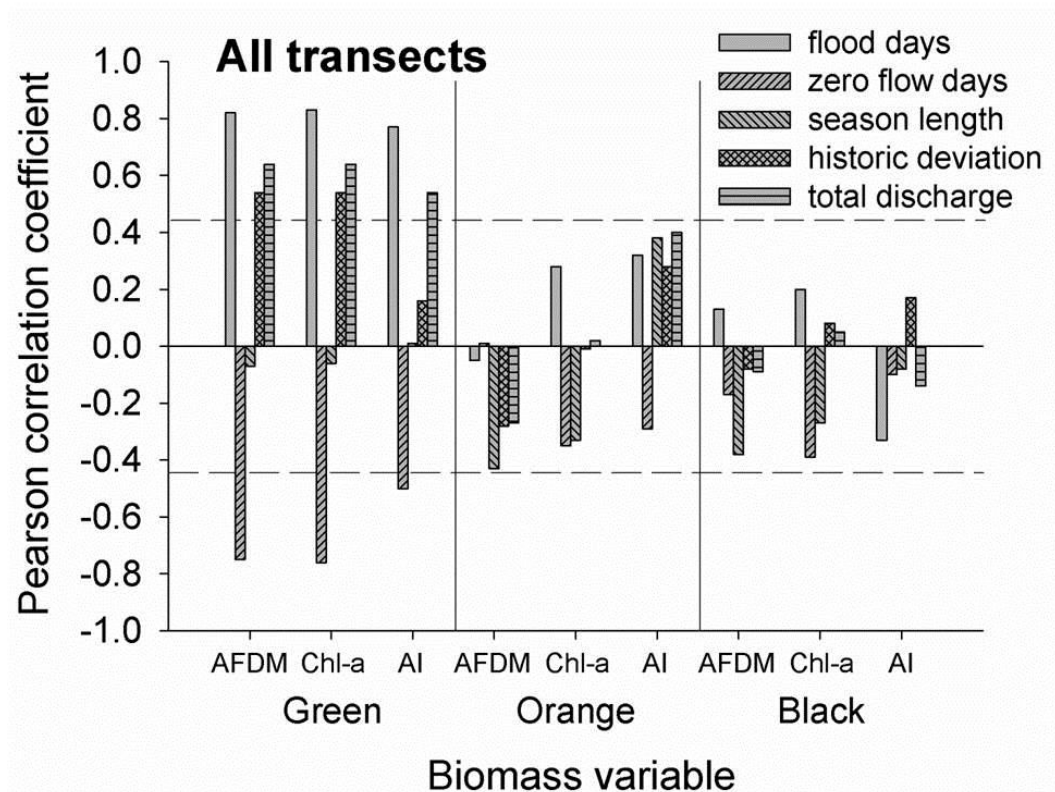
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Supplemental Figure 1. Square-root transformed ash-free dry mass (AFDM), chlorophyll-a (Chl-a), and the autotrophic index (AI = Chl-a:AFDM) for green, orange, and black mat types for all transects collected over the study period. Points are averaged values for each transect for each season. Grey-filled circles indicated data from high coverage transects, and unfilled circles are data from low coverage transects. The corresponding smoothed trend line is superimposed on each figure, and dotted lines indicate 95% confidence intervals.

Supplemental Table 1. Smoothed model statistical output for all compiled transects, including the model estimate, adjusted R², model p-value, parameter F-statistic, and parameter p-value. Shaded boxes are those models with p-values greater than 0.05.

Parameter coefficients for mat biomass from all transects						
Parametric coefficients				Significance of smooth terms		
parameter	estimate	t-value	p-value	adj R ²	F-value	p-value
G_AFDM	0.60	3.19	<0.01	-0.39	3.87	0.01
G_Ch1-a	0.53	3.97	<0.01	-0.55	4.55	0.01
G_AI	0.88	12.18	<0.01	0.32	6.42	<0.01
O_AFDM	1.59	8.34	<0.01	0.63	6.68	<0.01
O_Ch1-a	1.48	9.30	<0.01	0.76	12.66	<0.01
O_AI	0.76	17.89	<0.01	0.74	2.12	0.12
B_AFDM	3.81	9.04	<0.01	0.80	6.63	<0.01
B_Ch1-a	3.01	15.37	<0.01	1.00	17.18	<0.01
B_AI	0.86	25.15	<0.01	0.96	7.45	<0.01



Supplemental Figure 2. Bar graphs of Pearson correlation coefficients showing the strength and direction of correlations between hydrologic parameters and mat biomass for all compiled transects. PCC's (y-axis) were calculated by comparing ash-free dry mass (AFDM), chlorophyll-a (Chl-a), and the autotrophic index ($AI = Chl-a:AFDM$) of different mat types (x-axis) with hydrologic indices (in legend). The sign of the coefficient indicates whether the relationship is positive or negative, and dotted horizontal lines roughly indicate significance of correlations at $p = 0.05$.

Supplemental Table 2. AIC_c output and adjusted R² values for linear models describing green, orange, and black mat AFDM and Chl-a for all compiled transects. Shown are only those models with weights greater than or equal to 10% (Royall 1997). AIC indicates Akaike's Information Criterion, k indicates the number of parameters (including intercept and error terms), ΔAIC_c is the difference between the AIC_c value and the lowest AIC_c value, AIC_cWt is the relative likelihood that the model is the best approximating model, Cum.Wt is the cumulative weight, and LL is log likelihood. Variable abbreviations are as follows: "floods" = flood days, "season" = season length, "zeros" = zero flow days, "historic" = historic deviation, and "total_dis" = total discharge.

Models for all transects	k	AIC _c	ΔAIC _c	AIC _c Wt	Cum.Wt	LL	adj R ²
G_AFDM							
floods + season + total_dis + historic	6	-60.30	0	0.87	0.87	39.36	0.92
floods + season + zeros + total_dis + historic	7	-56.10	4.20	0.11	0.98	39.69	0.92
G_ChI-a							
floods + season + total_dis + historic	6	-49.80	0	0.88	0.88	34.13	0.92
floods + season + zeros + total_dis + historic	7	-45.50	4.34	0.10	0.98	34.40	0.92
O_AFDM							
floods + season + zeros + total_dis	6	-14.40	0	0.43	0.43	16.44	0.75
total_dis + historic + zeros + season	6	-14.30	0.15	0.40	0.83	16.36	0.75
O_ChI-a							
total_dis + historic + zeros + season	6	0.70	0	0.65	0.65	8.88	0.76
season + total_dis + zeros	5	3.85	3.15	0.13	0.78	5.22	0.67
floods + season + zeros + total_dis	6	3.85	3.15	0.13	0.91	7.30	0.72
B_AFDM							
total_dis + historic + zeros + season	6	5.56	0	0.78	0.78	6.45	0.70
B_ChI-a							
floods + season + zeros + total_dis	6	47.85	0	0.37	0.37	-14.7	0.82
floods + season + zeros	5	48.00	0.15	0.35	0.72	-16.9	0.79
floods + season + zeros + historic	6	48.72	0.87	0.24	0.96	-15.1	0.81

REFERENCES

- Alger, A.S., McKnight, D.M., Spaulding, S.A., Tate, C.M., Shupe, G.H., Welch, K.A., Edwards, R., Andrews, E.D., and House, H.R. 1997. Ecological processes in a cold desert ecosystem: the abundance and species distribution of algal mats in glacial meltwater streams in Taylor Valley, Antarctica. Institute of Arctic and Alpine Research Occasional Paper 51.
- Arblaster, J., and Meehl, G. 2006. Contributions of external forcings to Southern Annular Mode trends. *Journal of Climate* 19: 2896-2905.
- Barrett, J.E., Virginia, R.A., Wall, D.H., Doran, P.T., Fountain, A.G., Welch, K.A., and Lyons, W.B. 2008. Persistent effects of a discrete warming event on a polar desert ecosystem. *Global Change Biology* 14: 1-13.

- Biggs, B.J.F., Goring, D.G., and Nikora, V.I. 1998. Subsidy and stress responses of stream periphyton to gradients in water velocity as a function of community growth form. *Journal of Phycology* 34: 598-607.
- Biggs, B.J.F., and Thomsen, H.A. 1995. Disturbance in stream periphyton by perturbations in shear stress: Time to structural failure and differences in community resistance. *Journal of Phycology* 31: 233-241.
- Bonilla, S., Villeneuve, V., and Vincent, W.F. 2005. Benthic and planktonic algal communities in a high arctic lake: pigment structure and contrasting responses to nutrient enrichment. *Journal of Phycology* 41: 1120-1130.
- Burnham, K.P., and Anderson, D.R. 2002. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. New York: Springer New York, 488.
- Cardinale, B.J., Palmer, M.A., Swan, C.M., Brooks, S., and Poff, N.L. 2002. The influence of substrate heterogeneity on biofilm metabolism in a stream ecosystem. *Ecology* 83: 412–422.
- Chapman, W.L., and Walsh, J.E. 2007. A synthesis of Antarctic temperatures. *Journal of Climate* 20: 4096–4117.
- Clausen, B., and Biggs, B.J.F. 2000. Flow variables for ecological studies in temperate streams: groupings based on covariance. *Journal of Hydrology* 237: 184-197.
- Conovitz, P.A., McKnight, D.M., MacDonald, L.H., Fountain, A.G., and House, H.R. 1998. Hydrologic processes influencing streamflow variation in Fryxell Basin, Antarctica. In Prisco, J.C., Ed. *Ecosystem Dynamics in a Polar Desert: The McMurdo Dry Valleys, Antarctica*, Antarctic Research Series Vol. 72. Washington, D.C.: American Geophysical Union, 93-108.
- Cozzetto, K.D., Bencala, K.E., Gooseff, M.N., and McKnight, D.M. 2013. The influence of stream thermal regimes and preferential flow paths on hyporheic exchange in a glacial meltwater stream. *Water Resources Research* 49: 1-18.
- Cozzetto, K., McKnight, D., Nylen, T., and Fountain, A. 2006. Experimental investigations into processes controlling stream and hyporheic temperatures, Fryxell Basin, Antarctica. *Advances in Water Resources* 29: 130-153.
- Cullis, J.D., Gillis, C.A., Bothwell, M.L., Kilroy, C., Packman, A., and Hassan, M. 2012. A conceptual model for the blooming behavior and persistence of the benthic mat-forming diatom *Didymosphenia geminata* in oligotrophic streams. *Journal of Geophysical Research: Biogeosciences* (2005–2012) 117: G2.
- Cullis, J.D.S., Stanish, L.F., and McKnight, D.M. 2014. Diel flow pulses drive particulate organic matter transport from microbial mats in a glacial meltwater stream in the McMurdo Dry Valleys. *Water Resources Research* 50.

- Davis, J.M., Baxter, C.V., Minshall, G.W., Olson, N.F., Tang, C., and Crosby, B.T. 2013. Climate-induced shift in hydrological regime alters basal resource dynamics in a wilderness river ecosystem. *Freshwater Biology* 58: 306-319.
- Dodds, W.K., and Biggs, B.J.F. 2002. Water velocity attenuation by stream benthic algae in relation to growth form and architecture. *Journal of the North American Benthological Society* 21: 2-15.
- Dodds, W.K., Gido, K.B., Whiles, M.R., Fritz, K.M., and Matthews, W.J. 2004. Life on the edge: the ecology of Great Plains prairie streams. *Bioscience* 54: 205-216.
- Dodds, W.K., Gudder, D.A., and Mollenhauer, D. 1995. The ecology of *Nostoc*. *Journal of Phycology* 31: 2-18.
- Doran, P.T., Priscu, J.C., Lyons, W.B., Walsh, J.E., Fountain, A.G., McKnight, D.M., Moorhead, D.L., Virginia, R.A., Wall, D.H., Clow, G.D., Fritsen, C.H., McKay, C.P., and Parsons, A.N. 2002. Antarctic climate cooling and terrestrial ecosystem response. *Nature* 415: 517-520.
- Doran, P.T., McKay, C.P., Fountain, A.G., Nylen, T., McKnight, D.M., Jaros, C., and Barrett, J.E. 2008. Hydrologic response to extreme warm and cold summers in the McMurdo Dry Valleys, East Antarctica. *Antarctic Science* 20: 499-509.
- Esposito, R.M.M., Horn, S.L., McKnight, D.M., Cox, M.J., Grant, M.C., Spaulding, S.A., Doran, P.T., and Cozzetto, K.D. 2006. Antarctic climate cooling and response of diatoms in glacial meltwater streams. *Geophysical Research Letters* 33: L07406.1-L07406.4.
- Fountain, A.G., Lyons, W.B., Burkins, M.B., Dana, G.L., Doran, P.T., Lewis, K.J., McKnight, D.M., Moorhead, D.L., Parsons, A.N., Priscu, J.C., Wall, D.H., Wharton, R.A., and Virginia, R.A. 1999. Physical controls on the Taylor Valley ecosystem, Antarctica. *Bioscience* 49: 961-971.
- Francoeur, S.N., and Biggs, B.J.F. 2006. Short-term effects of elevated velocity and sediment abrasion on benthic algal communities. *Hydrobiologia* 561: 59-69.
- Fritz, K.M., and Dodds, W.K. 2005. Harshness: characterisation of intermittent stream habitat over space and time. *Marine and Freshwater Research* 56: 13-23.
- Fuller, F.L., Doyle, S., Levy, L., Owens, J., Shope, E., Vo, L., Wolyniak, E., Small, M.J., and Doyle, M.W. 2011. Impact of regulated releases on periphyton and macroinvertebrate communities: the dynamic relationship between hydrology and geomorphology in frequently flooded rivers. *River Research and Applications* 27: 630-645.
- Gooseff, M.N., McKnight, D.M., Doran, P., Fountain, A.G., and Lyons, W.B. 2011. Hydrological connectivity of the landscape of the McMurdo Dry Valleys, Antarctica. *Geography Compass* 5/9: 666-681.

- Gooseff, M.N., McKnight, D.M., Runkel, R.L., and Vaughn, B.H. 2003. Determining long time-scale hyporheic zone flow paths in Antarctic streams. *Hydrological Processes* 17: 1691-1710.
- Grimm, N.B., and Fisher, S.G. 1989. Stability of periphyton and macroinvertebrates to disturbance by flash floods in a desert stream. *Journal of the North American Benthological Society* 8: 293-307.
- Harrell Jr, F.E., and Dupont, C. 2014. Hmisc: Harrell Miscellaneous. R package version 3.14-5. Available at <http://cran.r-project.org/web/packages/Hmisc/index.html>. Accessed 26 Oct 2014.
- Hart, D.D., Biggs, B.J.F., Nikora, V.I., and Flinders, C.A. 2013. Flow effects on periphyton patches and their ecological consequences in a New Zealand river. *Freshwater Biology* 58: 1588-1602.
- Hawes, I. 1989. Filamentous green algae in freshwater streams on Signy Island, Antarctica. *Hydrobiologia* 172: 1-18.
- Hawes, I., and Brazier, P. 1991. Freshwater stream ecosystems of James Ross Island, Antarctica. *Antarctic Science* 3: 265-271.
- Hawes, I., Howard-Williams, C., and Vincent, W.F. 1992. Desiccation and recovery of Antarctic cyanobacterial mats. *Polar Biology* 12: 587-594.
- Hawes, I., and Howard-Williams, C. 1998. Primary production processes in streams of the McMurdo Dry Valleys, Antarctica. In Priscu, J.C., Ed. *Ecosystem Dynamics in a Polar Desert: The McMurdo Dry Valleys, Antarctica*, Antarctic Research Series Vol. 72. Washington, D.C.: American Geophysical Union, 129-140.
- House, H.R., McKnight, D.M., and von Guerard, P. 1995. The influence of stream channel characteristics on stream flow and annual water budgets for lakes in Taylor Valley. *Antarctic Journal of the United States*. 30: 284-287.
- Howard-Williams, C., and Hawes, I. 2007. Ecological processes in Antarctic inland waters: interactions between physical processes and the nitrogen cycle. *Antarctic Science* 19: 205-217.
- Howard-Williams, C., Priscu, J.C., and Vincent, W.F. 1989. Nitrogen dynamics in two Antarctic streams. *Hydrobiologia* 172: 51-61.
- Howard-Williams, C., Vincent, C.L., Broady, P.A., and Vincent, W.F. 1986. Antarctic stream ecosystems: Variability in environmental properties and algal community structure. *Internationale Revue der Gesamten Hydrobiologie und Hydrographie* 71: 511-544.

- Huntington, T.G. 2006. Evidence for intensification of the global water cycle: Review and synthesis. *Journal of Hydrology* 319: 83-95.
- Huryn, A.D., Slavik, K.A., Lowe, R.L., Parker, S.M., Anderson, D.S., and Peterson, B.J. 2005. Landscape heterogeneity and the biodiversity of Arctic stream communities: a habitat template analysis. *Canadian Journal of Fisheries and Aquatic Sciences* 62: 1905-1919.
- Jaros, C.L. 2003. Temperature-elevation effect on glacial meltwater generation in dry valley streams, Antarctica. Master's Thesis, University of Colorado.
- Koch, J.C., McKnight, D.M., and Neupauer, R.M. 2011. Simulating unsteady flow, anabranching, and hyporheic dynamics in a glacial meltwater stream using a coupled surface water routing and groundwater flow model. *Water Resources Research* 47: W05530.
- Kohler, T.J., Heatherly II, T.N., El-Sabaawi, R.W., Zandonà, E., Marshall, M.C., Flecker, A.S., Pringle, C.M., Reznick, D.N., and Thomas, S.A. 2012. Flow, nutrients and light availability influence Neotropical epilithon biomass and stoichiometry. *Freshwater Science* 31: 1019-1034.
- Kumar, S., Spaulding, S.A., Stohlgren, T.J., Hermann, K.A., Schmidt, T.S., and Bahls, L.L. 2009. Potential habitat distribution for the freshwater diatom *Didymosphenia geminata* in the continental US. *Frontiers in Ecology and the Environment* 7: 415-420.
- Lionard, M., Péquin, B., Lovejoy, C., and Vincent, W.F. 2012. Benthic cyanobacterial mats in the high Arctic: multi-layer structure and fluorescence responses to osmotic stress. *Frontiers in Microbiology* 3(140). doi: 10.3389/fmicb.2012.00140
- Lorenzen, C, and Jeffrey, S. 1980. Determination of chlorophyll in seawater. UNESCO technical papers in marine science 35: 1-20.
- McKnight, D.M., Alger, A.S., Tate, C.M., Shupe, G., and Spaulding, S. 1998. Longitudinal patterns in algal abundance and species distribution in meltwater streams in Taylor Valley, Southern Victoria Land, Antarctica. In Prisco, J.C., Ed. *Ecosystem Dynamics in a Polar Desert: The McMurdo Dry Valleys, Antarctica*, Antarctic Research Series Vol. 72. Washington, D.C.: American Geophysical Union, 109–127.
- McKnight, D.M., Niyogi, D.K., Alger, A.S., Bomblies, A., Conovitz, P.A., and Tate, C.M. 1999. Dry Valley streams in Antarctica: ecosystems waiting for water. *Bioscience* 49: 985-995.
- McKnight, D.M., and Tate, C.M. 1997. Canada Stream: A glacial meltwater stream in Taylor Valley, South Victoria Land, Antarctica. *Journal of the North American Benthological Society* 16: 14-17.
- McKnight, D.M., Tate, C.M., Andrews, E.D., Niyogi, D.K., Cozzetto, K., Welch, K., Lyons, W.B., and Capone, D.G. 2007. Reactivation of a cryptobiotic stream ecosystem in the

- McMurdo Dry Valleys, Antarctica: A long-term geomorphological experiment. *Geomorphology* 89: 186-204.
- Miller, M.P., McKnight, D.M., Cullis, J.D., Greene, A., Vietti, K., and Liptzin, D. 2009. Factors controlling streambed coverage of *Didymosphenia geminata* in two regulated streams in the Colorado Front Range. *Hydrobiologia* 630: 207-218.
- Niyogi, D.K., Tate, C.M., McKnight, D.M., Duff, J.H., and Alger, A.S. 1997. Species composition and primary production of algal communities in Dry Valley streams in Antarctica: Examination of the functional role of biodiversity. In Lyons WB, Howard Williams C, Hawes I, Eds. *Ecosystem processes in Antarctic ice-free landscapes*. Rotterdam: Balkema, 171-179.
- Parker, S.M., and Huryn, A.D. 2011. Effects of natural disturbance on stream communities: a habitat template analysis of arctic headwater streams. *Freshwater Biology* 56: 1342-1357.
- Poff, N.L., Allen, J.D., Bain, M.B., Karr, J.R., Prestegard, K.L., Richter, B.D., Sparks, R.E., and Stromberg, J.C. 1997. The natural flow regime: A paradigm for river conservation and restoration. *Bioscience* 47: 769-784.
- Poff, N.L., Olden, J.D., Merritt, D.M., and Pepin, D.M. 2007. Homogenization of regional river dynamics by dams and global biodiversity implications. *Proceedings of the National Academy of Sciences* 104: 5732-5737.
- R Core Team. 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available at <http://www.R-project.org/>.
- Richard, Y., Rouault, M., Pohl, B., Cr  tat, J., Duclot, I., Taboulot, S., Reason, C.J.C., Macron, C., and Buiron, D. 2013. Temperature changes in the mid- and high- latitudes of the Southern Hemisphere. *International Journal of Climatology* 33: 1948-1963.
- Rochera, C., Fernandez-Valiente, E., Van de Vijver, B., Rico, E., Toro, M., Vincent, W.F., Quesada, A., and Camacho, A. 2013. Community structure and photosynthetic activity of benthic biofilms from a waterfall in the maritime Antarctica. *Polar Biology* 36: 1709-1722. doi: 10.1007/s00300-013-1388-3
- Royall, R.M. 1997. *Statistical evidence: a likelihood paradigm*. New York, NY: Chapman and Hall.
- Simon, K.S., Townsend, C.R., Biggs, B.J.F., and Bowden, W.B. 2004. Temporal variation of N and P uptake in 2 New Zealand streams. *Journal of the North American Benthological Society* 24: 1-18.
- Spaulding, S., and Elwell, L. 2007. Increase in nuisance blooms and geographic expansion of the freshwater diatom *Didymosphenia geminata*. Open-File Report 2007-1425. U.S. Geological Survey.

- Stanish, L.F., Kohler, T.J., Esposito, R.M.M., Simmons, B.L., Nielsen, U.N., Wall, D.H., Nemergut, D.R., and McKnight, D.M. 2012. Extreme streams: flow intermittency as a control on diatom communities in meltwater streams in the McMurdo Dry Valleys, Antarctica. *Canadian Journal of Fisheries and Aquatic Sciences* 69: 1405-1419.
- Stanish, L.F., Nemergut, D.R., and McKnight, D.M. 2011. Hydrologic processes influence diatom community composition in Dry Valley streams. *Journal of the North American Benthological Society* 30: 1057-1073. doi: 10.1899/11-008.1
- Steinman, A., Lamberti, G.A., and Leavitt, P.R. 1996. Biomass and pigments of benthic algae. In Hauer, F.R., and Lamberti, G.A., Eds. *Methods in stream ecology*. 2nd ed. San Diego, CA: Academic Press, 357-379.
- Stevenson, R.J. 1996. The stimulation and drag of current. In Stevenson, R.J., Bothwell, M.L., and Lowe, R.L., Eds. *Algal ecology: freshwater benthic ecosystems*. San Diego, CA: Academic Press, 321-340.
- Strickland, J.D.H., and Parsons, T.R. 1972. *A practical handbook of seawater analysis*, 2nd edition. Ottawa, Ontario: Fisheries Research Board of Canada Bulletin 167.
- Thompson, D.W.J., Solomon, S., Kushner, P.J., England, M.H., Grise, K.M., and Karoly, D.J. 2011. Signatures of the Antarctic ozone hole in Southern Hemisphere surface climate change. *Nature Geoscience* 4: 741-749.
- Treonis, A.M., Wall, D.H., Virginia, R.A. 1999. Invertebrate biodiversity in Antarctic dry valley soils and sediments. *Ecosystems* 2: 482-492.
- Vincent, W.F., Downes, M.T., Castenholz, R.W., and Howard-Williams, C. 1993. Community structure and pigment organisation of cyanobacteria-dominated microbial mats in Antarctica. *European Journal of Phycology* 28: 213-221.
- Vincent, W.F., and Howard-Williams, C. 1986. Antarctic stream ecosystems: physiological ecology of a blue-green algal epilithon. *Freshwater Biology* 16: 219-233.
- Virginia, R.A., Wall, D.H. 1999. How soils structure communities in the Antarctic Dry Valleys. *Bioscience* 49: 973-983.
- Walsh, J.E. 2009. A comparison of Arctic and Antarctic climate change, present and future. *Antarctic Science* 21: 179-188.
- Welschmeyer, N.A. 1994. Fluorometric analysis of chlorophyll a in the presence of chlorophyll b and pheopigments. *Limnology and Oceanography* 39: 1985-1992. doi: 10.4319/lo.1994.39.8.1985.

- Whitton, B.A., Ellwood, N.T.W., and Kawecka, B. 2009. Biology of the freshwater diatom *Didymosphenia*: a review. *Hydrobiologia* 630: 1-37.
- Wolman, M.G. 1954. A method for sampling coarse river-bed material. *Transactions of the American Geophysical Union* 35: 951-956.
- Wood, S. 2014. mgcv: Mixed GAM Computation Vehicle with GCV/AIC/REML smoothness estimation. R package version 1.8-3. Available at <http://cran.r-project.org/web/packages/mgcv/index.html>. Accessed 26 Oct 2014.
- Zuur, A.F., Ieno, E.N., and Elphick, C.S. 2010. A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution* 1: 3-14.
- Zuur, A.F., Ieno, E.N., and Smith, G.M. 2007. *Analysing Ecological Data*. New York, NY: Springer New York, 672 pp.
- Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., and Smith, G.M. 2009. *Mixed effects models and extensions in ecology with R*. New York, NY: Springer New York, 574 pp.

CHAPTER IV

ISOTOPIC AND ELEMENTAL COMPOSITION OF ANTARCTIC STREAM MICROBIAL COMMUNITIES

ABSTRACT

Quantifying isotopic and elemental composition of primary producers is a useful approach to investigating ecosystem foodwebs and mass balance. However, taxonomic differences and habitat heterogeneity complicate mixing models, and disentangling these variables in field studies is difficult. Here we test how taxonomic identity, in-stream position, and dissolved carbon (C), nitrogen (N) and phosphorus (P) concentrations influence microbial mat elemental composition and isotopic ratios in the simple stream systems of the McMurdo Dry Valleys, Antarctica. We found that black *Nostoc* mats consistently exhibited the highest C:N, C:P, and N:P ratios, while orange *Oscillatorian* mats contained greater P (lower in C:P and N:P). Green chlorophyte mats had the most depleted $\delta^{13}\text{C}$ signatures and orange mats the most enriched, which may suggest greater utilization of CO_2 in the former and HCO_3^- use in the latter. Black mats were intermediate in $\delta^{13}\text{C}$ ratios, but enriched in $\delta^{15}\text{N}$ compared to other types indicating N-fixation. When minimum adequate GLS models were created for mat variables, elemental and isotopic ratios were sometimes strongly correlated to water column nutrient concentrations and physical location within the stream channel. Molar C:P and N:P ratios decreased with greater P availability, but most pronounced for orange mats. Black mat elemental composition was most correlated with N. All mat $\delta^{15}\text{N}$ signatures became more depleted as bulk N concentration increased, and became more enriched in downstream versus upstream sites. Collectively, these data suggest that mat types assimilate nutrients as a function of the life histories of dominant taxa, as well as habitat use which creates differential access to nutrients, and aid in our understanding of stream biogeochemical cycles and ecosystem connectivity.

INTRODUCTION

Stable isotopes and nutrient ratios are common ecological tools used to investigate energy flow, nutrient retention, and foodweb structure in freshwater systems. Differences in taxonomic composition among primary producers may contribute to variability in isotopic discrimination and thus signature, as well as to differences in elemental and nutrient turnover rates (e.g. Finlay 2004, Hart et al. 2013, Peipoch et al. 2014), which may have large consequences in foodweb modeling (Zah et al. 2001, Dodds et al. 2014). However, while taxonomic differences have been studied in culture (Montoya and McCarthy 1995, Needoba et al. 2003) and in lake phytoplankton (Vuorio et al. 2006), they remain poorly studied in streams. This is largely because individual contributions are difficult to account for, since conglomerate “epilithon” and “periphyton” are most often sampled (Abe et al. 2014, Dodds et al. 2014), and generally include varying proportions of detritus, fungi, and heterotrophic bacteria in addition to algae. Primary producers are furthermore strongly influenced by riparian/watershed activity (Kohler et al. 2012) and higher trophic levels (McIntyre et al. 2008, Kohler et al. 2011), making the controlled field study of taxonomic responses to environmental variability in streams challenging.

The McMurdo Dry Valleys (MDV) are an ice-free area of Antarctica that is underlain with several hundred meters of permafrost (McGinnis and Jensen 1971), with an active layer of 20-40 cm over most of the valleys (Gooseff et al. 2013). During summer, glacial melt generated from 24-hour radiation contributes to glacial melt which creates an extensive network of streams that flow for several weeks and drain into closed basin lakes, reactivating resident microbial mat communities (McKnight et al. 1999, McKnight et al. 2007). Because primary production within Antarctic streams is distributed among distinct chlorophyte, filamentous cyanobacteria, and N-fixing *Nostoc* “mat types” (Hawes 1989, Alger et al. 1997, Davey 1993, Rochera et al. 2013), broad taxon-specific responses that arise from environmental variability may be possible to

investigate. Furthermore, a lack of allochthonous inputs, riparian vegetation, and substantial grazer biomass makes the MDVs an ideal place to study the in-stream processes controlling autochthonous energy in a controlled manner (Treonis et al. 1999, Gooseff et al. 2011).

The streams of the MDVs are nutrient conduits, transporting elements from source glaciers to closed basin lakes on the valley floors. The resident microbial communities intercept (Howard-Williams et al. 1989, Hawes and Schwarz 1999, McKnight et al. 2004) and transform (Gooseff et al. 2004) elements and compounds *en route*. These communities also act as nutrient sinks, and high biomass streams generally have lower nutrient concentrations (McKnight et al. 2004, Barrett et al. 2007). Given the relative scarcity of organic material in the MDVs (Barrett et al. 2006, Barrett et al. 2007), mats are organic matter and nutrient hotspots both within streams and across the landscape. Despite this, it is not understood what controls nutrient storage in stream mats, and reported nutrient ratios are limited to those in Barrett et al. (2007) and McKnight et al. (2007), both of which are limited in spatial scope and taxonomic diversity. Since the lakes obtain most of their water and nutrients from streams (esp. SRP, Foreman et al. 2004), mechanisms responsible for the transport, storage, and release of nutrients in streams are important to understanding MDV ecology and connectivity (Neumann et al. 1998, Lawson Knoepfle et al. 2009, Lyons et al. 2013).

Stream chemistry in the MDVs varies in two predictable ways: First, solute concentrations tend to increase downstream as a function of accumulated weathering (Welch et al. 2010), while nutrients tend to decrease longitudinally in stream with high mat biomass because of uptake (Howard-Williams et al. 1989, McKnight et al. 1998, McKnight et al. 2004). Therefore, longer streams may have greater alkalinity, though lower nutrient concentrations than shorter streams. Furthermore, streams in Taylor Valley have greater nitrogen concentrations

inland and away from the coast, while phosphorus is greater in streams that occur on Ross Sea glacial deposits (Barrett et al. 2007, Welch et al. 2010). While nutrient cycling outcomes at the stream reach scale have been more explored (Gooseff et al. 2004, Koch et al. 2010), longitudinal patterns in nutrient cycling and stoichiometry could vary at the valley scale, as has been observed for MDV soils (Barrett et al. 2006, 2007) and mosses (Ball and Virginia 2014). This alternation in nutrient availability is a unique opportunity to investigate the influence of nutrients on the elemental signatures of microbial mats without artificial augmentation.

In this study we ask three questions: First, do the different MDV stream mat types have unique isotopic and elemental signatures given habitat and taxonomic differences? Secondly, are there broad patterns in the elemental and isotopic composition of mat types as a function of longitudinal position (upstream or downstream)? Lastly, are the signatures of mats explained by ambient nutrient concentrations across diverse Taylor Valley streams? We expect elemental and isotopic compositions to be distinct for a given mat type due to differences in structure, taxonomy, and habitat. N-fixing mat types should have a $\delta^{15}\text{N}$ signature near 0, and non-N-fixing communities should become more depleted where nutrient concentrations are higher (Peterson et al. 1997, Brabandere et al. 2007) since biological processes discriminate against the heavier species (Montoya and McCarthy 1995). Lastly, mats may exhibit “luxury consumption” with increasing nutrient concentration resulting in greater nutrient content (Sterner and Elser 2002), though well-developed cyanobacterial mats may exhibit less stoichiometric plasticity due to diffusion limitation and internal mat cycling (Varin et al. 2010, Vincent and Quesada 2012).

METHODS

Site description

Taylor Valley (Figure 1) is situated along a geologic chronosequence with phosphorus (P) in greater abundance on glacial deposits enriched in apatite, while nitrogen (N) is more abundant to the west as a result of atmospheric deposition that has accumulated over time (Michalski et al. 2005, Barrett et al. 2007, Bate et al. 2008, Welch et al. 2010). Intensifying this gradient is the relatively longer streams of the Lake Fryxell Basin nearer the coast compared to the shorter inland streams of the Lake Bonney and Lake Hoare Basins. Longer streams allow for more weathering, resulting in greater P concentrations, yet lower N as a result of greater microbial uptake, while the opposite may be observed in shorter streams. These relationships are reflected in the long-term water chemistry sampling of MCMLTER streams (Welch et al. 2010), as well as in the MDV lakes into which they drain (Priscu 1995, Morgan-Kiss et al. 2006, Foreman et al. 2004).

Primary production in MDV streams is distributed across four microbial community types (“mats” for brevity), which differ in appearance, habitat, and the dominate taxon (Howard-Williams et al. 1986, Alger et al. 1997). Orange mats form a thick layer over the benthic substrata of the main channel, are comprised of filamentous cyanobacteria genera such as *Oscillatoria* Vaucher ex Gomont, *Leptolyngbya* Anagnostidis & Komárek, *Wilmottia* Strunecký, Elster & Komárek and *Microcoleus* Desmazières ex Gomont. Red mats are almost identical in habitat preference and taxonomic composition to orange mats, but have a dense, rubbery outer layer that is distinctly red or pink, and are more sparsely distributed throughout the MDV. Black mats are comprised of the N-fixing cyanobacterial genus *Nostoc* Vaucher ex Bornet & Flahault and live at streams margins where they are not submerged, but utilize hyporheic water and periodic flood pulses. Lastly, green mats comprised of chlorophytes such as *Prasiola* Meneghini form streamers or tufts along the sides and undersides of rocks (Alger et al. 1997). Heterotrophic

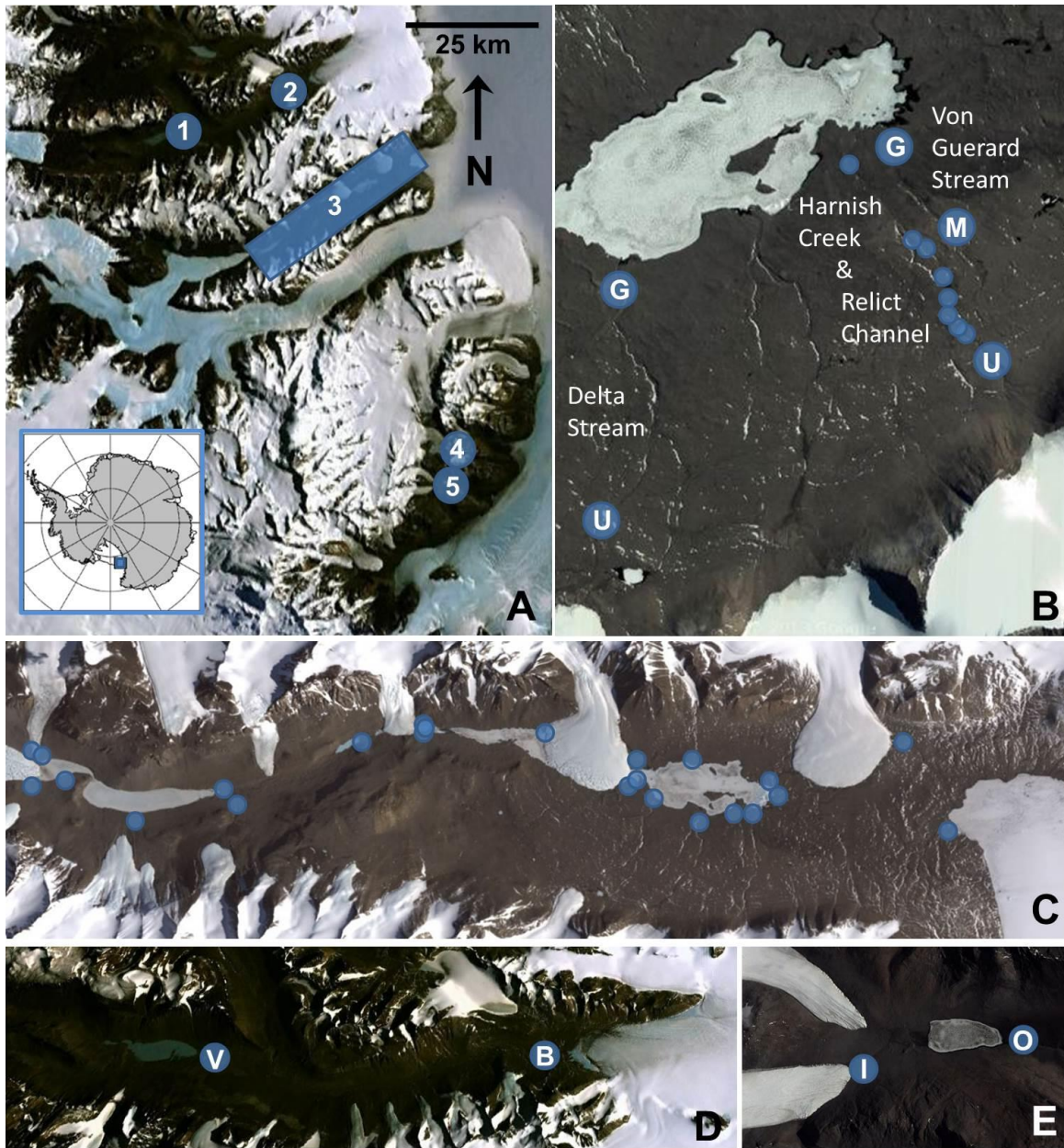


Figure 1. Panel A: Map of the McMurdo Dry Valleys with inset of the Antarctic Continent. Highlighted areas include 1) Onyx River at Lake Vanda, 2) Onyx River at Lake Brownworth, 3) Taylor Valley, 4) Garwood Valley, and 5) Miers Valley. Panel B: Detail of the southeast side of Lake Fryxell. The upper/gage locations are labeled for Delta stream at left and upper/middle/gage locations for Von Guerard Stream at right. Blue circles left of Von Guerard indicate locations of samples taken along the longitudinal reach of the Relict Channel, starting at the Von Guerard stream diversion and ending at the Harnish Creek stream gage. Panel C: Detail of Taylor Valley with Taylor Glacier to the left (southwest) and the Ross Sea coast to the right (northeast). Blue circles indicate the approximate location of samples taken at stream outlets. Panel D: Detail of the Wright Valley showing Lake Vanda (V) and Brownworth (B) locations. Panel E: Detail of Miers Valley showing the Lake Miers inlet (I) and outlet (O) sample locations. Map data ©2015 Google.

bacteria and diatoms live within all mat types, though at lower abundances than dominate taxa.

Microbial mats dominate nutrient removal at high biomass, and mat assimilation and uptake of NO_3^- may be orders of magnitude higher than hyporheic denitrification (Gooseff et al. 2004). However, the hyporheic zone is important to nutrient cycling and mineral weathering in the MDV, especially in streams with low mat biomass (Koch et al. 2010), and can be readily observed compared to temperate streams. Furthermore, hyporheic water has been shown to significantly differ in nutrient concentration from the water column (McKnight et al. 2004), and substantial dissimilatory reduction (Gooseff et al. 2004, McKnight et al. 2004) and weathering (Maurice et al. 2002) has been measured in hyporheic sediments. Since access to hyporheic water differs by mat type as a function of habitat use (Figure 2), mats may not be equally affected by overall differences in streamwater chemistry. For example, green mats are only able to utilize water column nutrients, while black mats primarily utilize hyporheic water, and orange mats likely are able to utilize both sources given their position at the stream bottom.

Sample collection

To test how longitudinal location within a stream influences the elemental and isotopic composition of mats based on presumed differences in chemistry, duplicate samples of black and orange mats were taken along established transects in the Relict Channel, which is a long term experimental stream segment consisting of a reactivated stream reach that receives diverted water from Von Guerard Stream (Figure 1B, see map in McKnight et al. 2007). The channel contains high mat biomass, and the stream flows through several large wetland areas before emptying into Harnish Creek downstream. To test upstream versus downstream patterns in elemental stoichiometry and isotopic signatures across sites, mats were sampled at upper, middle,

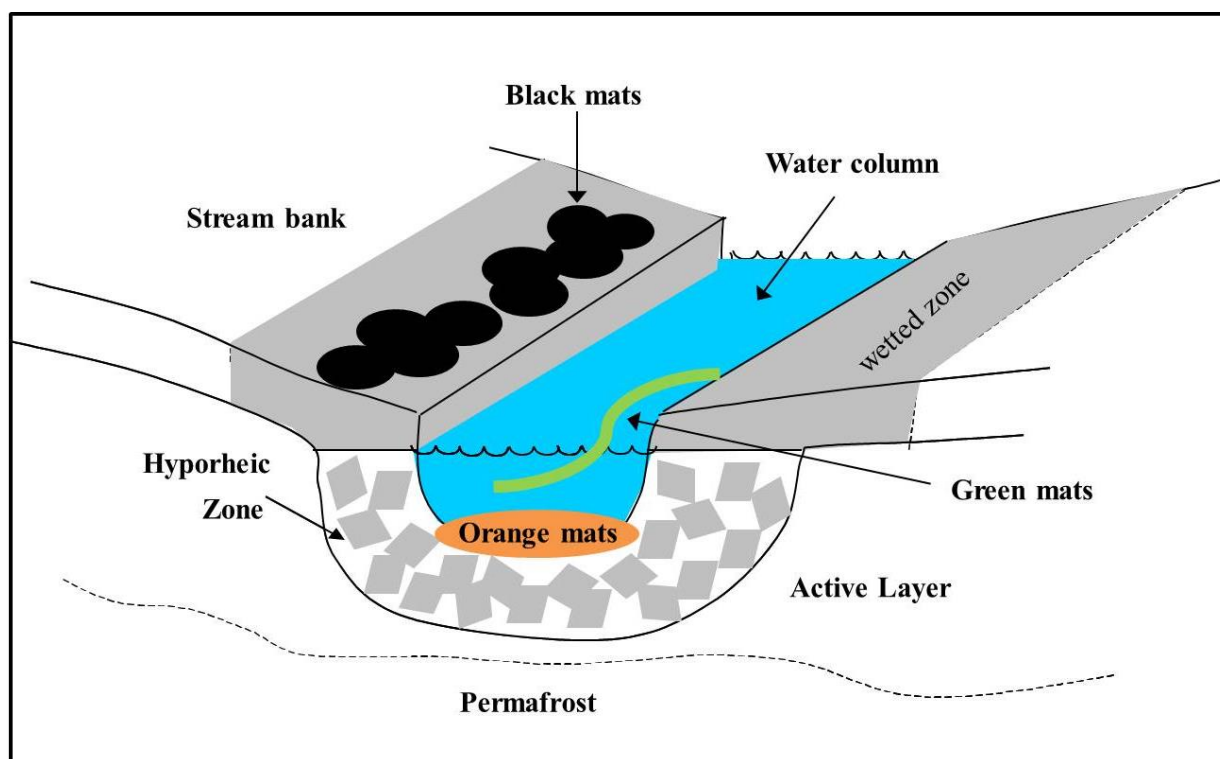


Figure 2. Conceptual diagram of habitat use by different mat types in McMurdo Dry Valley streams. Adapted from Gooseff et al. (2002).

and downstream sites in Von Guerard (VG) Stream, and upstream and downstream sites in Delta Stream and Harnish Creek within Taylor Valley (Figure 1B, Table 1, see maps in McKnight et al. 1998). The Onyx River in Wright Valley, the longest river in Antarctica at over 30 km long, was additionally sampled at the Lower Brownworth and Lake Vanda outlet sites (Figure 1D, see Howard-Williams et al. 1997, Green et al. 2005). Lastly, the inlet (Adams Stream) and outlet to Lake Miers was sampled in Miers Valley (Figure 1E).

To test how microbial mats respond to differing nutrient concentrations along a geochemical gradient, we additionally surveyed a variety of sites across Taylor Valley, and along established transects monitored by the McMurdo Long-Term Ecological Research (MCMLTER) program if possible (Figure 1C, Table 1), which predominately occur at stream outlets near discharge gaging stations. Lastly, mat material was also taken from a tributary of Garwood

Table 1: Stream sample site, valley, outlet basin, GPS coordinates, mat types collected (B = black, O = orange, G = green, R = red), and year samples were taken. Streams from Taylor Valley are presented roughly in order from the Ross Sea. (*) Indicates unofficial names, (**) indicates stoichiometry was only analyzed for green and red mats, but biomass was measured for all mat types. As the Relict Channel has multiple transects, see McKnight et al. (2007) for locations.

Sample site	Valley	Drainage basin	Latitude (S)	Longitude (W)	Mat types	Summer sampled
Wales Stream	Taylor	Ross Sea	-77.57942	163.50575	B,O	2012-13
Commonwealth Stream	Taylor	Ross Sea	-77.56361	163.38256	B,O,G	2011-12
Von Guerard Stream Gage	Taylor	Fryxell	-77.60925	163.25408	B,O,G	2012-13
Von Guerard Stream Middle	Taylor	Fryxell	-77.61930	163.28836	B,O,G	2012-13
Von Guerard Stream Upper	Taylor	Fryxell	-77.63445	163.30612	B,O,G	2012-13
Aiken Creek	Taylor	Fryxell	-77.60153	163.29089	B,O	2011-12
Green Creek	Taylor	Fryxell	-77.62441	163.05936	B,O,G	2011-12
Harnish Creek	Taylor	Fryxell	-77.61221	163.23265	B,O	2012-13
Relict Channel	Taylor	Fryxell	<i>See McKnight et al. 2007</i>		B,O	2012-13
Delta Stream Upper	Taylor	Fryxell	-77.65315	163.09972	B,O,G	2012-13
Delta Stream Gage	Taylor	Fryxell	-77.62533	163.10954	B,O,G	2012-13
Canada Stream Gage	Taylor	Fryxell	-77.61325	163.05322	B,O,G,R	2011-12
Canada Stream Delta*	Taylor	Fryxell	-77.61462	163.06999	B,O,G,R	2012-13
Lost Seal Stream	Taylor	Fryxell	-77.59595	163.24454	O	2012-13
Bowles Creek	Taylor	Fryxell	-77.62327	163.05776	B,O,G	2011-12
Huey Creek	Taylor	Fryxell	-77.60231	163.12361	B,O	2012-13
Andersen Creek	Taylor	Hoare	-77.62131	162.90698	O	2012-13
House Stream	Taylor	Hoare	-77.64286	162.74227	O	2011-12
McKay Creek	Taylor	Hoare	-77.64409	162.74612	O	2011-12
Wharton Creek	Taylor	Hoare	-77.64465	162.74507	B,O	2012-13
Popplewell Stream**	Taylor	Mummy	-77.65760	162.67897	B,O,R	2012-13
Priscu Stream	Taylor	Bonney	-77.69637	162.53614	O	2012-13
Bohner Stream	Taylor	Bonney	-77.69628	162.56392	O,G	2011-12
Lyons Creek Tributary	Taylor	Bonney	-77.72685	162.27992	O	2012-13
Lawson Creek	Taylor	Bonney	-77.72036	162.26878	B,O,G,R	2011-12
Little Sharpe Creek**	Taylor	Bonney	-77.72131	162.25880	B,O	2012-13
Wormherder Creek	Taylor	Bonney	-77.72598	162.31551	O	2011-12
Garwood River Tributary	Garwood	Ross Sea	-78.02302	163.91661	B,O,G	2012-13
Adams Stream	Miers	Miers	-78.10424	163.73604	B,O,G	2011-12
Miers River at Outlet	Miers	Ross Sea	-78.09943	163.90204	O,G	2011-12
Onyx River at Vanda	Wright	Vanda	-77.52403	161.69627	O	2011-12
Onyx River at Brownworth	Wright	Vanda	-77.44306	162.66423	O	2011-12

Stream in Garwood Valley due to an abundance of more rare green mats, which was used in comparisons of mat characteristics.

All samples were taken in late December and January of 2012 and 2013. Up to four different mat types were found at each site, and up to five different samples were taken for each mat type. Mats were carefully lifted off the substrate with a spatula, and four subsamples were taken from the lifted mat with a brass cork borer (#13, 227 mm²). Subsamples were placed in stream water and transported back to the laboratory, where they were prepared for the following analyses; ash-free dry mass (AFDM), chlorophyll-a (Chl-a), C:N:P stoichiometry, and $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopes. All samples were dewatered onto Whatman® GF/F filters, wrapped in foil, and frozen at -20°C until analysis.

Biomass

Biomass was determined as Chl-a and AFDM. Chl-a was measured by extracting samples in 90% buffered acetone for 24 hours (Welschmeyer, 1994) and analyzed on a Turner Designs 10-AU field fluorometer (Turner Designs, Sunnyvale, California). AFDM subsamples were dried at 55°C for 24 h (or until a constant mass was achieved), weighed, burned at 450°C for 4 h and reweighed, then rewetted and dried to determine mass loss caused by hydration of sediments (Steinman et al. 1996). An autotrophic index (AI) was created by dividing Chl-a by AFDM. All biomass analyses were performed in Crary Laboratory at McMurdo Station.

Elemental analyses

The C:N:P and isotope subsamples were dried in an oven at 50-55 °C, then ground to a fine powder and homogenized. Carbonates were removed by a fumigation method similar to Hedges and Stern (1984). A second aliquot was not acidified in order to estimate inorganic carbon, as well as to confirm that $\delta^{15}\text{N}$ signatures were not altered by acidification. Percent C and N content

was measured using a CE 1500 Elemental Analyzer (CE Instruments Ltd., Wigan, UK) and $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope ratios were obtained with Finnigan-MAT Delta Plus XL mass spectrometer at the Center for Stable Isotope Biogeochemistry operated by the University of California, Berkeley. The %P aliquot was ashed in a muffle furnace at 500 °C for one hour, digested with 1N HCl, and analyzed as orthophosphate with a Lachat QuikChem 8500 Flow Injection Analyzer (Hach Company, Loveland, Colorado) by the Kiowa lab at the University of Colorado, Boulder (Murphy and Riley 1962). A spinach standard (#1570a) was analyzed approximately every 10 samples to ensure method accuracy and digestion success. The resulting values were then converted to molar C:N, C:P, and N:P ratios.

Water chemistry

Stream water for chemistry analyses was collected opportunistically for each stream throughout the flow season, and water samples were always collected concurrently with biomass sampling. Raw water was collected in triple-rinsed 250 mL Nalgene® bottles for nutrients samples, and 125 mL pre-combusted amber glass bottles for dissolved organic carbon (DOC). Samples for titration alkalinity, which in the MDVs are primarily bicarbonate (DIN), were collected in 20 mL plastic scintillation vials, and analyzed as in Welch et al. (2010). Water for nutrient analysis was filtered from the raw water sample on glass-fiber filters and frozen for later analysis at the field station. DOC was filtered, acidified using concentrated HCl, and stored at 4°C. All chemistry analyses were performed at the Crary Laboratory at McMurdo Station following the methods outlined in Welch et al. (2010) using a Lachat QuikChem 8000 FIA autoanalyzer with Omnion 3.0 software (Loveland, CO) optimized for low concentrations. DOC was measured on a Shimadzu TOC-V CPN Total Organic Carbon Analyzer with a detection limit of 0.1 mg L⁻¹.

Dissolved inorganic nitrogen (DIN) was calculated as the sum of NH_3^+ , NO_2^- and NO_3^- , and soluble reactive phosphorus is hereafter abbreviated as SRP.

Nutrient concentrations in streamwater are variable throughout the flow season. Initial “first flow” concentrations can be orders of magnitudes higher in concentration than those later in the summer as the streambed is flushed, and increased discharges lead to nutrient dilution and microbial uptake from reactivated mats. Because of this, water chemistry measurements are “snapshots in time”, and concentrations do not necessarily reflect values over a season. We therefore took the mean values of all water chemistry samples collected during a summer for each transect to use in our analysis. Additionally, given the known long-term relationship between nutrient concentration and the location within Taylor Valley (Welch et al. 2010), we measured the distance a particular site is to the Ross Sea coast (near New Harbor camp) using Google Earth©. The distance between longitudinal transects within streams were estimated in a similar fashion. All water chemistry and mat biomass values are available online at www.mcmlter.org.

Statistical Analyses

Prior to analyses, we conducted an exploratory data analysis (Zuur et al. 2009, Zuur et al. 2010) to identify potential outliers and characterize the distribution of data. All variables that were not normally distributed were $\log_{10}(x)$ -transformed. To assess relationships between chemistry, mat coverage, and distance from the Ross Sea coast, average values of Taylor Valley data were compared using simple linear regression (*lm*) models, with only one value per stream per season used in the analysis. High and low coverage transect data and categorization methodology were

taken from (Alger et al. 1997). Linear regression models linking biomass variables to the distance from the Ross Sea coast were not averaged.

The importance of categorical variables was tested by constructing linear mixed-effects (*lmer*) models using the *lme4* R package (Bates et al. 2014). “Mat type” was tested as a fixed effect with “basin” and “stream” as random variables using the un-averaged full dataset, while “upstream/downstream” location was tested on a reduced dataset including only data with paired upstream/downstream locations, and included “mat type” and “stream” as random variables. In this dataset, the middle transect was omitted in the case of VG Stream, and Relict Channel transects 0 and 1 were combined as the “upstream” locations, and were compared against Harnish Creek as the “downstream” location for both statistics and Figure 5. P-values were estimated using the *lmerTest* R package (Kuznetsova et al. 2014).

To assess individual mat responses to environmental data throughout Taylor Valley, generalized least squares (GLS) models were created for the unaveraged data of each mat type using the *nlme* R package (Pinheiro et al. 2006). These models allow variance functions to account for heteroscedasticity, allowing variances to differ by category. Microbial mat stoichiometry (C:N, C:P, and N:P) and isotopic ratios ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) were modeled as a function of drainage basin, nutrient availability (DIN, SRP, DOC) and the ratio of Chl-a to AFDM (AI) for each mat type (black, orange, and green). Minimum adequate models were not created for red mats due to low *n* size, and biomass variables were not modeled due to an inability to disentangle effects of nutrients on mats from the effects of mat uptake on dissolved nutrients. All nitrogen species were combined as DIN because NO_3^- was collinear with DIN, and NH_4^+ and NO_2^- were low and often undetectable. Similarly, the N:P ratio of streamwater was omitted due to correlation with SRP, and distance from the coast was omitted due to high

correlations with both DIN and SRP. Lake basin, mat type, and stream identity were included as random variables and/or variance functions if they improved model fit, as assessed by AIC values.

Optimal model structure for each variable was investigated by using restricted maximum likelihood (REML) on global models (with all fixed-effects variables) to test for the best combination of random effects (i.e. variance structures), and model improvement was assessed by a reduction in AIC values. Once GLS models were created, non-significant fixed-effects terms were removed through backward selection to retrieve the minimum adequate model. This was achieved by using maximum likelihood (ML), and the elimination of terms was justified by conducting likelihood ratio (L-ratio) tests. Once the minimum adequate model was achieved (no more terms could justifiably be removed), the final model output was reported using REML (West et al. 2006). Finally, the significance of individual fixed effects terms was estimated using L-ratio tests (and switching to ML) which compare the minimum adequate model with the same model without the variable being tested. Significance was set at $\alpha = 0.05$, and all statistical analyses were performed using the R console, version 3.0.3 (R Core Team 2014).

RESULTS

Differences between mat types

All mat data were compiled from this study to test if mats differ in their biomass, stoichiometry, and isotopic composition. Chl-a (ANOVA, $F=41.274$, $p<0.001$) and AFDM (ANOVA, $F=132.11$, $p<0.001$) were significantly different between mat types (Figure 3). Black mats generally had greater values of AFDM and Chl-a than other mat types, and averaged $23.52 \text{ mg AFDM cm}^2$ ($SE \pm 1.02$) and $17.02 \text{ } \mu\text{g Chl-a cm}^2$ ($SE \pm 1.13$). Red mats had slightly greater

average AFDM with 25.83 mg AFDM cm² (SE ± 2.30), but lower Chl-a with 8.09 µg Chl-a cm² (SE ± 1.02). Orange mats averaged 9.85 mg AFDM cm² (SE ± 0.49) and 8.56 µg Chl-a cm² (SE ± 0.52). Green mats had the lowest average biomass values, with 3.21 mg AFDM cm² (SE ± 0.26) and 3.79 µg Chl-a cm² (SE ± 0.37). The ratios of these biomass metrics (AI=Chl-a:AFDM) was also different by mat type (ANOVA, F=15.554, p<0.001). Green mats had the greatest AI, with average values of 1.34 (SE ± 0.05), followed by orange mats (0.92, SE ± 0.04), black mats (0.76, SE ± 0.05), and red mats (0.32, SE ± 0.03).

Mat types also differed in their C:N (ANOVA, F=24.866, p<0.001), C:P (ANOVA, F=35.666, p<0.001) and N:P (ANOVA, F=55.357, p<0.001) stoichiometry (Figure 3). With few exceptions, C:N ratios were greater than the Redfield ratio (~7) for all mat types in all streams. Red mats had the greatest C:N ratios, and averaged 13.15 (SE ± 0.40). Other mat types had very similar average C:N values; 10.76 (SE ± 0.19) for black mats, 9.99 (SE ± 0.33) for green mats, and 9.61 (SE ± 0.14) for orange mats. For C:P ratios, orange mats were lower than all other mat types, and were consistently below the Redfield ratio of ~106 with an average of 60.39 (SE ± 6.69). The remaining mat types were more similar in their C:P ratios (and above Redfield ratio), with black mats 147.77 (SE ± 11.81), green mats 153.51 (SE ± 11.27), and red mats 159.65 (SE ± 29.94). All mats were below the Redfield ratio for N:P (~16) except for black mats, which was slightly above this value and averaged 17.25 (SE ± 1.04). Orange mats had the lowest average N:P ratios and averaged 6.12 (SE ± 0.41). Green and red mats were similar, and averaged 14.14 (SE ± 0.83) and 13.22 (SE ± 1.80), respectively.

Different mat types also differed in the type of assimilated elements (Figure 3). $\delta^{15}\text{N}$ signatures differed between mat types (ANOVA, F=66.948, p<0.001), with black mats having the most enriched -2.00 (SE ± 0.26) values and closest to the atmospheric standard. The

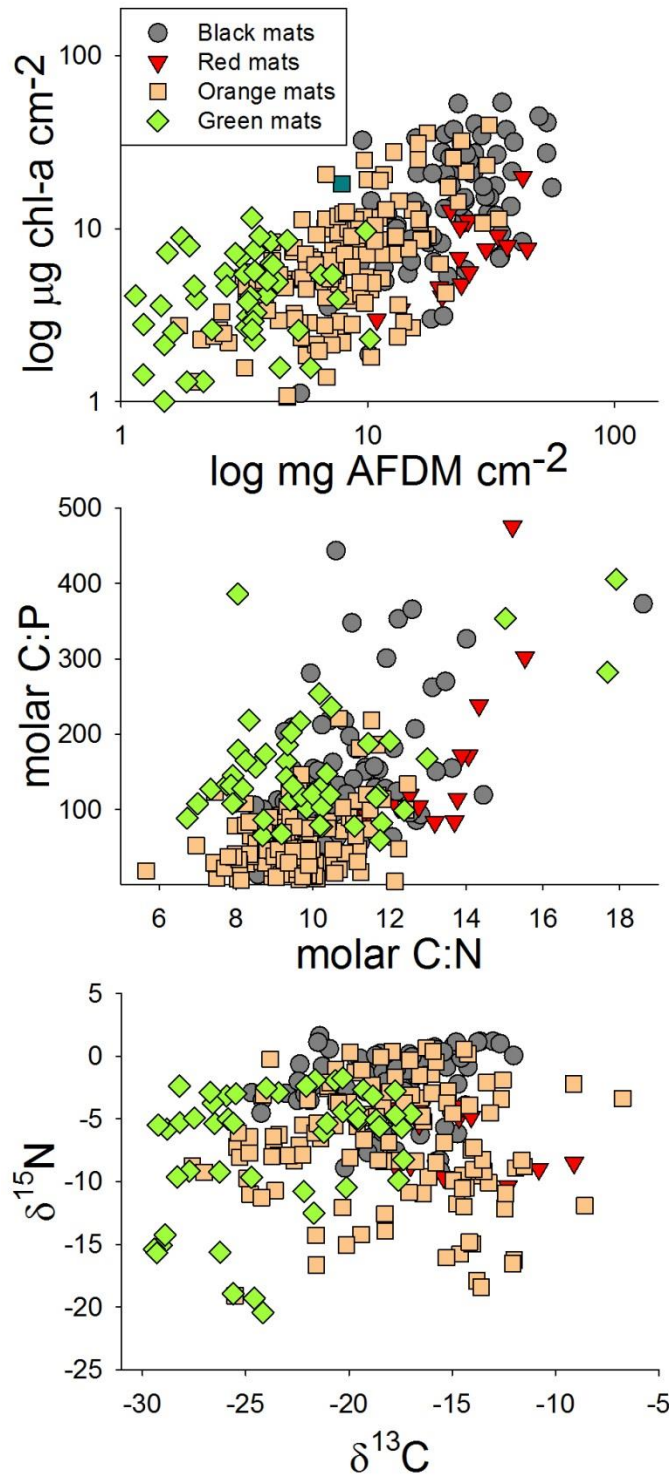


Figure 3: AFDM plotted against Chl-a, C:N plotted against C:P, and $\delta^{15}\text{N}$ plotted against $\delta^{13}\text{C}$ for the four different mats using all data from this study.

remaining mat types were very similar in their average $\delta^{15}\text{N}$ signatures, with -6.72 ($\text{SE} \pm 0.63$) for green mats, -6.54 ($\text{SE} \pm 0.38$) for orange mats, and -6.34 ($\text{SE} \pm 0.65$) for red mats. Ratios of $\delta^{13}\text{C}$ were also different between mat types (ANOVA, $F=30.362$, $p<0.001$). Green mats had lower $\delta^{13}\text{C}$ values than others, averaging -23.40 ($\text{SE} \pm 0.57$). Orange and black mats were similar in their average $\delta^{13}\text{C}$ values, with -18.13 ($\text{SE} \pm 0.40$) and -17.88 ($\text{SE} \pm 0.31$), respectively. Red mats had the most enriched $\delta^{13}\text{C}$ ratios, averaging -14.97 ($\text{SE} \pm 0.70$). Mat types also differed in their inorganic carbon content (ANOVA, $F=19.761$, $p<0.001$), with the highest values in black mats with about 3.13% on

average (± 0.55 SE). This was followed by red mats with 0.70% (± 0.47 SE), and orange mats with 0.40% (± 0.12 SE) inorganic C. Green mats had undetectable inorganic carbon (-0.82% , $\text{SE} \pm 0.54$), and actually had a negative average, likely because sample error increases with carbon

concentration in this calculation (Green mats average %C after acidification = 13.7%, red mats = 4.4, black mats = 4.7, and orange mats = 1.8).

Upstream/downstream comparisons

Water chemistry measurements taken over the last decade in VG Stream, which is representative of most streams on the south side of Lake Fryxell, indicates that SRP decreases from upstream to downstream locations, while DIN is relatively constant, though more variable at the outlet (Figure 4A). At the inlet and outlet locations of Lake Miers in Miers Valley, both DIN and SRP were greater at the inlet of the lake compared to the outlet (Figure 4B). At the Onyx River, the decade-averaged DIN was over twice as high at Lake Vanda compared to at Lake Brownworth, while SRP was similar between sites and at the limit of detection (Figure 4C).

To shed light onto longitudinal patterns in streams, orange and black mats were analyzed for individual transects over the Relict Channel, which were then plotted against their longitudinal location from the headwaters (Figure 4). Orange mat C:N was much lower than black mat C:N at headwaters, but the two converged on a value of roughly 9.5 about 500 m from the VG Upper algal transect, coinciding with the inlet to a large high-biomass wetland. Values remained similar for both mat types until reaching the Harnish Creek gage over 3000 m below. Orange mats had consistently lower C:P and N:P values throughout the channel, though values began to increase on approaching and leaving the broad wetland before returning to previous values (Figure 5). Black mats were more variable, but peaked in values before the peak in orange mats. Orange mats were initially more depleted in both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ ratios at headwaters compared to black mats. However, orange mats steadily increased in $\delta^{15}\text{N}$ from the headwaters until about transect 5 (the same as the peak for C:P and N:P), at which point they remained a

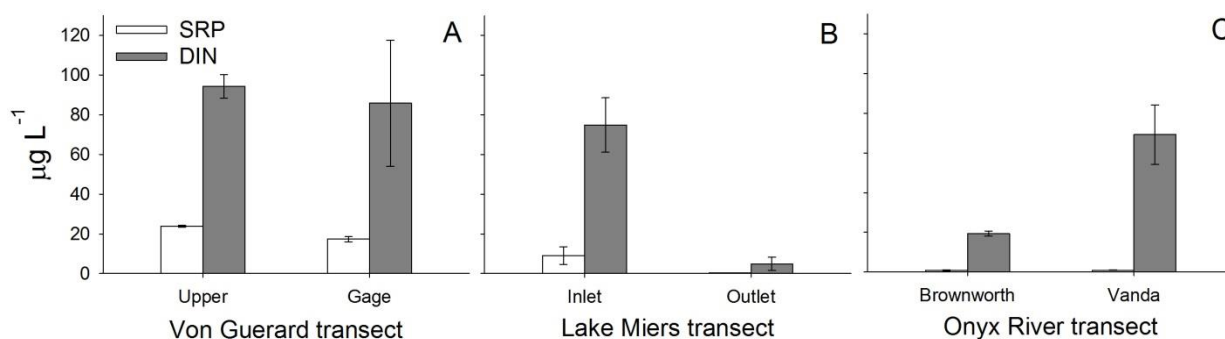


Figure 4: (A) Average DIN and SRP data for Von Guerard Upper (n=14) and Von Guerard Gage (n=39), (B) Lake Miers inlet (n=5) and outlet (n=3), and (C) the Onyx River at Lake Brownworth (n=45) and at Lake Vanda (n=47). Data are all samples taken over the last 10 years (2003-04 to 2012-13, mcmlter.org), and error bars indicate standard error.

constant value of about 0.5 along with black mats, which never deviated from this value. For $\delta^{13}\text{C}$, both mat types became more enriched over the transects associated with the slower moving water of the large wetlands, though again decrease at the Harnish Creek gage.

Mats from upstream and downstream locations of multiple streams were additionally compared to identify trends among sites. However, mat C:N:P stoichiometry had no clear, significant relationship between upstream and downstream location, and differences observed varied by mat type and the stream sampled (Figure 6). For example, the green and orange mats from Delta Stream, black mats from Harnish Creek, and orange mats from the Onyx River had greater C:N, C:P, and N:P ratios at upstream localities than did their downstream counterparts. This is in contrast to Delta Stream black mats, and green and orange mats from the inlet and outlet to Lake Miers, where C:N, C:P, and N:P increased from upstream to downstream (with the exception of the green mat, which was based upon a single sample). Similarly, orange mats in VG Stream and Harnish Creek showed modest increases in C:N:P stoichiometry from the headwaters to the outlet, while VG black mats showed modest decreases. All $\delta^{15}\text{N}$ ratios in mats

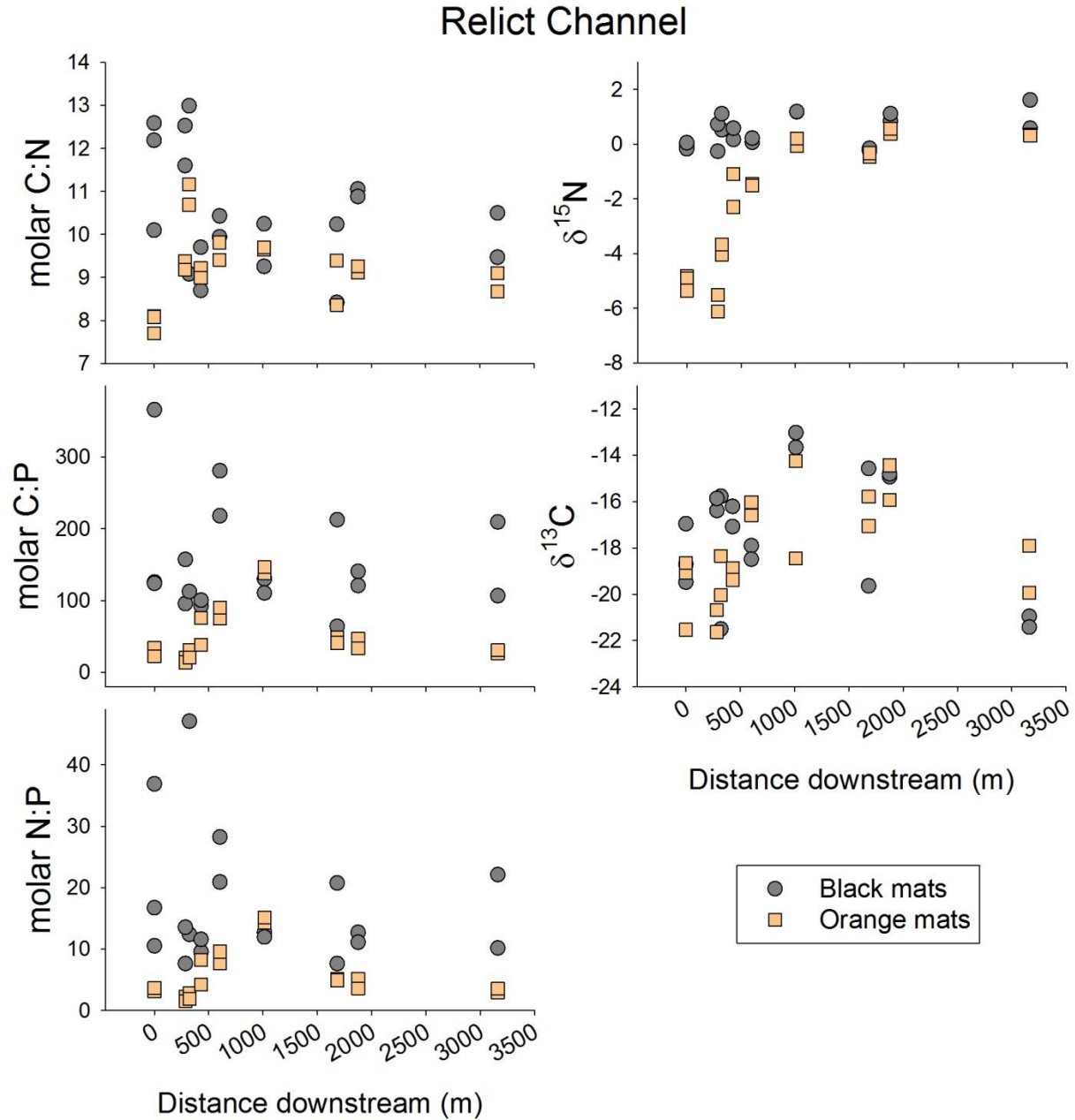


Figure 5: Molar C:N, C:P, N:P, $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ of black and orange mats from upstream (left) to downstream (right) transect sites in the Relict Channel, plotted as distance from the Von Guerard Upper algal transect.

became more enriched from upstream to downstream transects (ANOVA, $F = 9.822$, $p = 0.003$) with the exception of the Onyx River (Figure 6). In Von Guerard Stream, orange and green mats were more enriched from the upper to the middle and gage transects, while black mats were

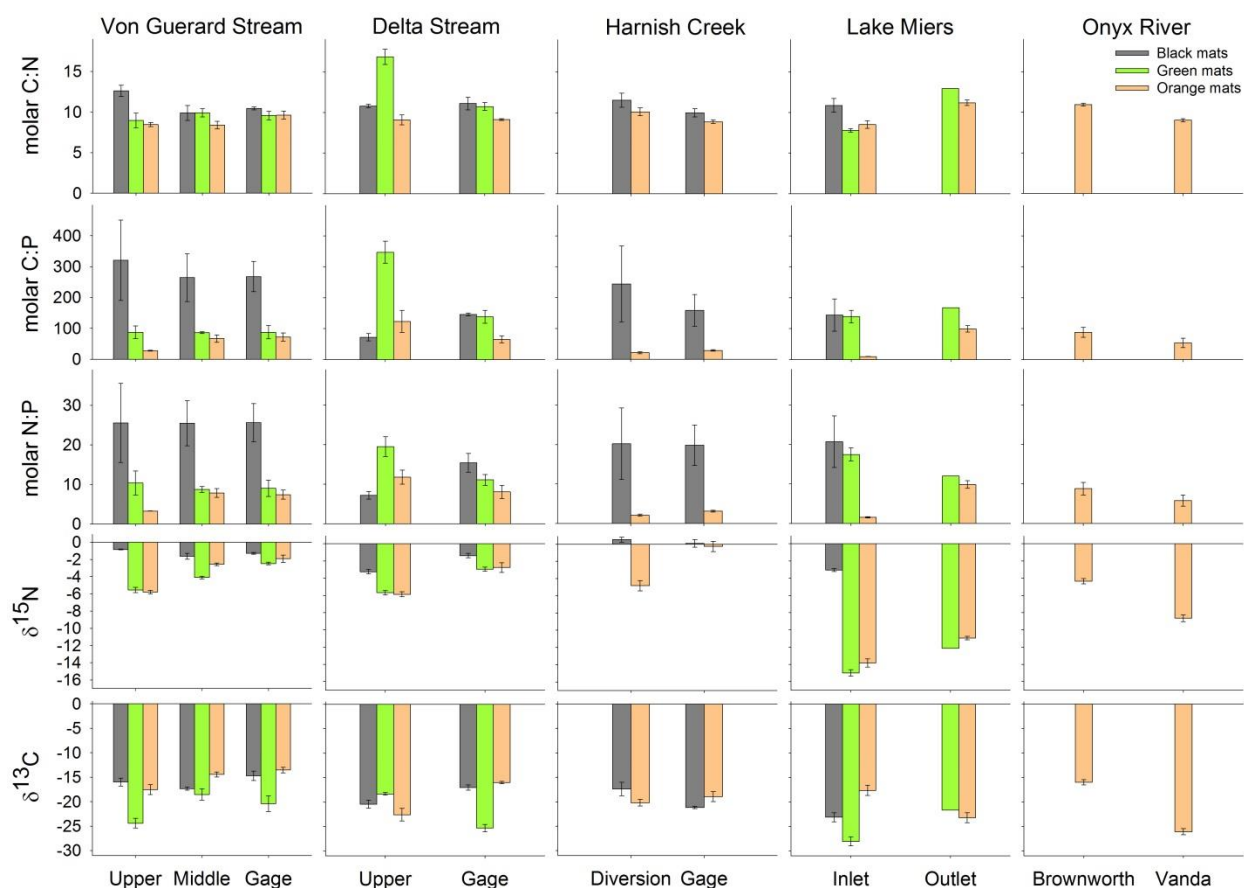


Figure 6: Molar C:N, C:P, N:P, $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ plotted for different mat types from upstream and downstream locations from five streams. See Figure 1 for transect locations.

stable or became more depleted between the upper and gage transects. In Delta stream, all mat types (black, orange, and green) were more enriched at the gage site than the upper site. Patterns were less clear for $\delta^{13}\text{C}$. Upper VG Stream and Delta Stream black and orange mats were more depleted in $\delta^{13}\text{C}$ than mats at the outlets, although this pattern was opposite for Harnish Creek black mats, Delta Stream green mats, and orange mats from Lake Miers and the Onyx River.

Mat characteristics and chemistry over Taylor Valley

Streams with abundant microbial mats (high coverage) were significantly lower in DIN (ANOVA, $F=7.452$, $df=38$, $p=0.010$), and significantly greater in DOC (ANOVA, $F=6.658$,

df=35, $p=0.014$) concentrations than streams with low mat abundance (low coverage). SRP concentrations were not significantly different between high and low coverage transects. All high coverage streams were within the Fryxell Basin. The position within Taylor Valley was furthermore strongly related to nutrient concentration. The distance from the Ross Sea coast was associated with significant increases in NO_3^- (Adj. $R^2=0.186$, $t=3.151$, $df=38$, $p=0.003$), although there was no significant relationship between NH_4^+ , NO_2^- , and physical location. Since the DIN was overwhelmingly comprised of NO_3^- , strong increases in DIN were observed with increasing distance from the coast (Figure 7, $t=3.194$, $df=38$, $p=0.003$). Conversely, concentrations of SRP decreased as the valley extends west ($t=-2.015$, $df=33$, $p=0.052$). As a result, the water column N:P ratio significantly increased with distance from the coast ($t=4.549$, $df=34$, $p<0.001$). Overall, most streams were above the Redfield ratio of ~ 16 , indicating that widespread P limitation is likely. Finally, concentrations of DOC decreased away from the coast ($t=-2.303$, $df=36$, $p=0.027$), but there was no pattern in alkalinity.

To assess differences in mat characteristics across diverse sites, mats were also sampled over Taylor Valley from the Ross Sea coast to Taylor Glacier. In general, the AFDM of mat types was poorly related to the distance to the coast, although green mat AFDM slightly decreased inland ($t=-2.227$, $p=0.03$). Orange ($t=-2.934$, $p=0.004$) and black ($t=-2.549$, $p=0.013$) mat Chl-a was greater near the Ross Sea (Figure 8), though there was no pattern for green mats. As a result, orange ($t=-3.296$, $p=0.001$) and black ($t=-3.827$, $p<0.001$) mat AI significantly decreased away from the Ross Sea. Green mat C:N decreased ($t=-4.881$, $p<0.001$), while black mat C:N increased over the same distance ($t=4.437$, $p<0.001$), and orange mat C:N was not significantly different over Taylor Valley (Figure 9). The C:P of all mat types increased towards

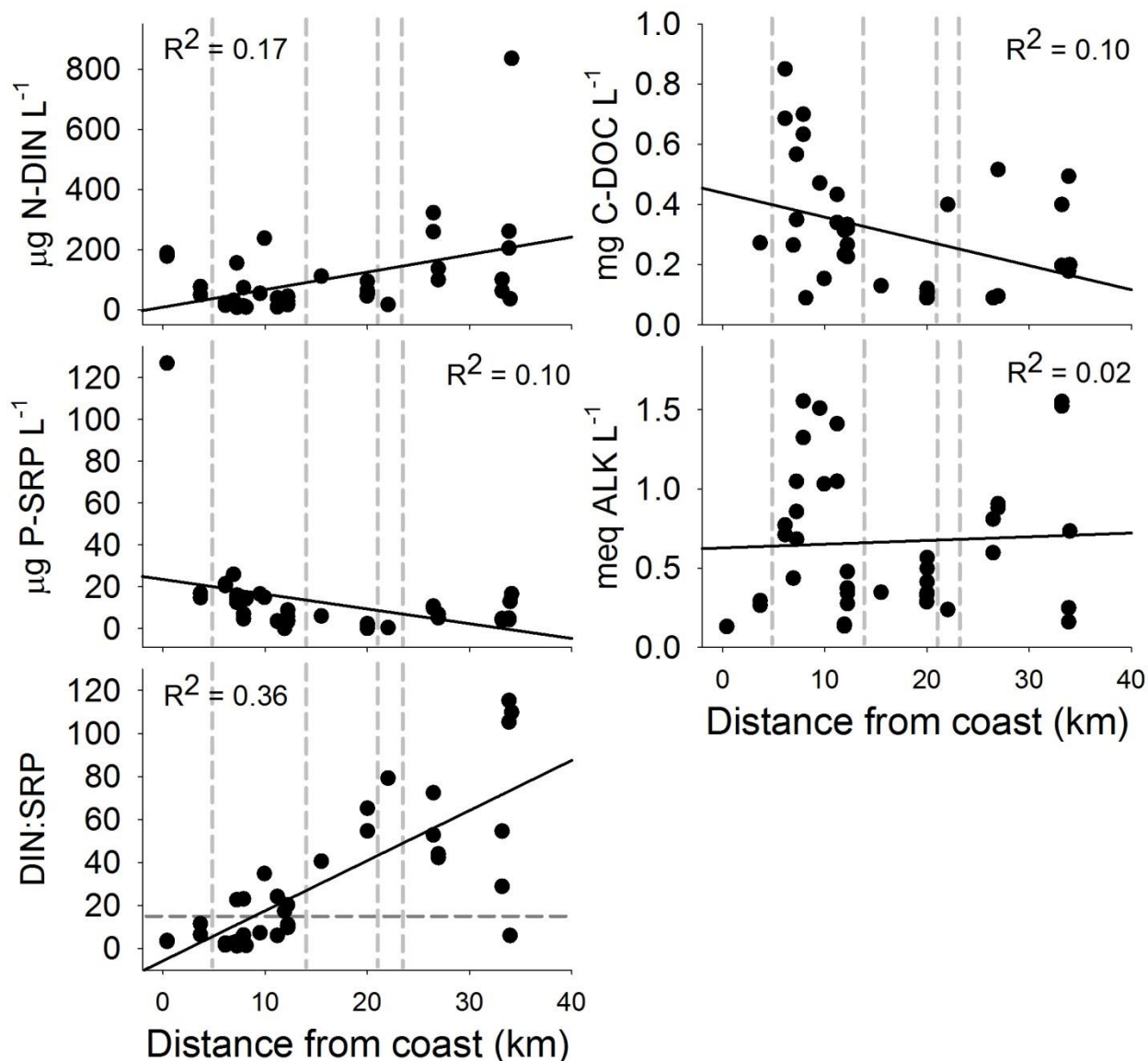


Figure 7: Dissolved inorganic nitrogen (DIN), soluble reactive phosphorus (SRP), the dissolved N:P ratio, dissolved organic carbon (DOC), and alkalinity plotted against the distance from the coast. Samples were taken during the 2011-12 and 2012-13 summers over the length of Taylor Valley. The dotted horizontal line on the bottom figure indicates Redfield Ratio of ~16. Grey vertical lines separate drainage basins, which from left to right includes the Ross Sea, Lake Fryxell, Lake Hoare, Mummy Pond, and Lake Bonney.

Taylor Glacier, although this relationship was only significant for orange mats ($t=2.176$, $p=0.032$). Green mat N:P ($t=3.407$, $p=0.001$) strongly increased with increasing distance from

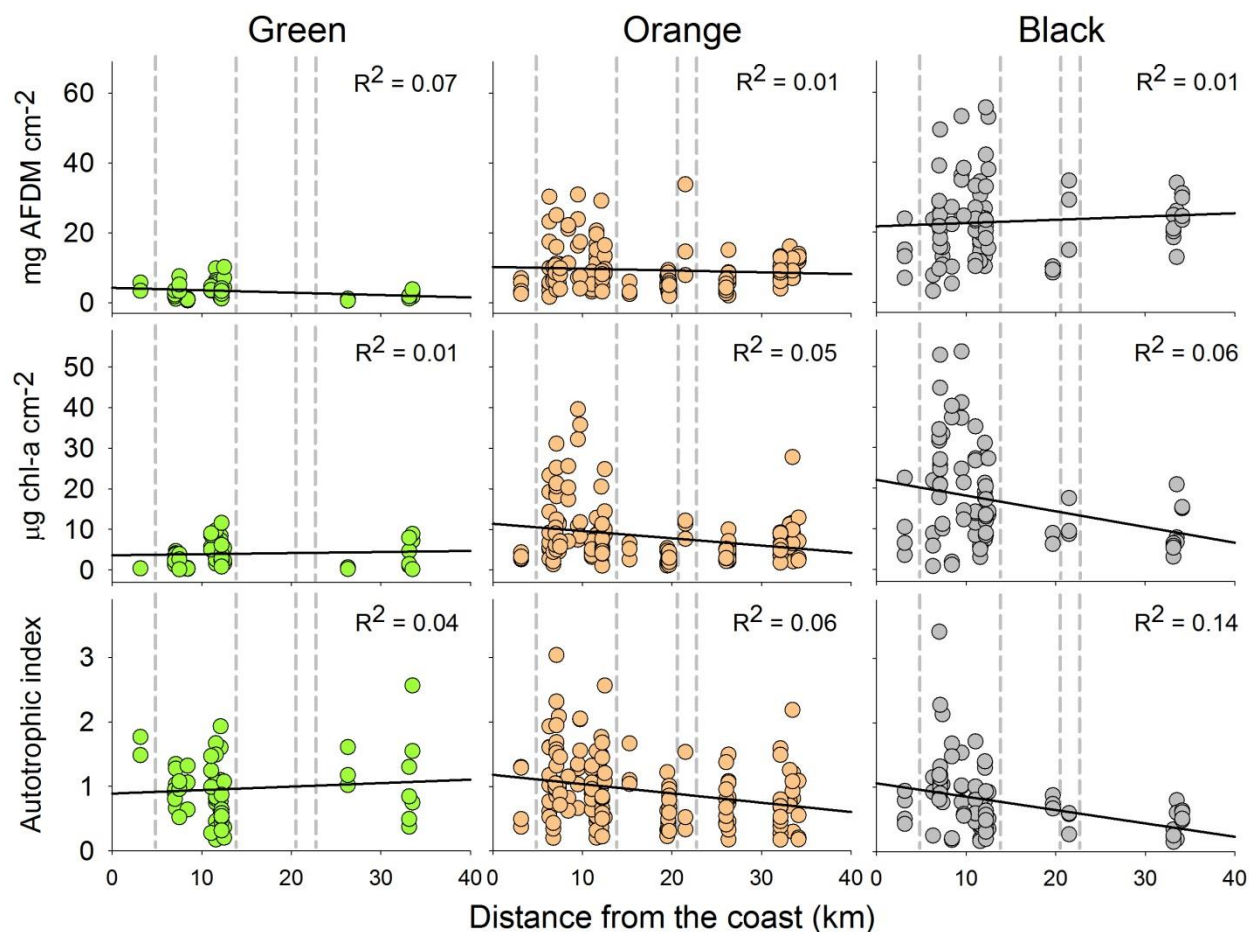


Figure 8: AFDM, Chl-a, and the autotrophic index plotted for green (left), orange (middle), and black (right) mats against the distance from the Ross Sea coast. Grey lines separate drainage basins, which from left to right includes the Ross Sea, Lake Fryxell, Lake Hoare, Mummy Pond, and Lake Bonney.

the coast, but there was no association in black or orange mats (Figure 9). All mat types were more depleted in $\delta^{15}\text{N}$ as distance from the coast increased (green: $t=-5.586$, $p<0.001$, orange: $t=-7.693$, $p<0.001$, black: $t=-7.164$, $p<0.001$). Only orange mats showed patterns in $\delta^{13}\text{C}$ signatures (Figure 10), and increased away from the coast to Taylor Glacier ($t=4.979$, $p<0.001$).

The distance from the coast was highly correlated with most mat variables, and because it was also collinear with SRP and DIN, it was omitted from global GLS models to elucidate relationships with specific nutrients. When minimum adequate models were created for green

Table 2: Minimum adequate general least squares (GLS) model output describing green mat characteristics. Abbreviations are as follows: df = degrees of freedom, loglike = log-likelihood, vf = variance function, SRP = soluble reactive phosphorus, DIN = dissolved inorganic nitrogen, DOC = dissolved organic carbon, and AI = autotrophic index.

Mat type	Variable	df	loglike	vf	Coefficients	Value	SE	t-value	p-value
Green	C:N	6	-44.978	~1 Basin	(Intercept)	7.696	0.193	39.801	0.000
					Basin(Fryxell)	2.341	0.299	7.838	0.000
					Basin(Ross)	0.945	0.232	4.073	0.000
	C:P	5	-2.927	~1 Basin	(Intercept)	4.971	0.064	77.120	0.000
					AI	-0.290	0.080	-3.627	0.001
	N:P	5	-7.475	none	(Intercept)	4.255	0.457	9.316	0.000
					Basin(Fryxell)	-0.456	0.123	-3.713	0.001
					Basin(Ross)	0.387	0.247	1.569	0.124
					SRP	-0.469	0.153	-3.064	0.004
	$\delta^{13}\text{C}$	18	-74.3825	~1 Stream	(Intercept)	-9.564	3.960	-2.415	0.022
					Basin(Fryxell)	7.467	1.527	4.891	0.000
					Basin(Ross)	1.550	1.929	0.804	0.428
					SRP	-8.581	1.890	-4.542	0.000
					DIN	1.860	0.846	2.197	0.035
					AI	-3.230	0.836	-3.863	0.001
	$\delta^{15}\text{N}$	7	16.28966	~1 Basin	(Intercept)	-3.258	0.181	-17.979	0.000
					Basin(Fryxell)	0.832	0.047	17.818	0.000
					Basin(Ross)	0.380	0.044	8.625	0.000
					SRP	0.305	0.063	4.837	0.000

mats, C:N was significantly different by drainage basin (Table 2, L-ratio=32.990, df=4, $p<0.001$), with greatest values in the Fryxell basin, and lowest values in the Bonney basin (Figure 9). C:P ratios were greatest for streams draining into the Ross Sea and lowest in the Fryxell basin, although basin was not included in the minimum adequate model. Green mat C:P was only significantly, and negatively, associated with AI (L-ratio=7.681, df=4, $p=0.006$). Basin of origin was important for green N:P ratios (L-ratio=21.648, df=3, $p<0.001$), and values were higher in the Ross Sea and Bonney basins than in the Fryxell basin. N:P ratios were further negatively related to SRP (L-ratio=9.281, df=4, $p=0.002$). Green mat $\delta^{13}\text{C}$ signatures significantly different by basin (L-ratio=9.203, d=15, $p=0.010$), with the highest values in the Fryxell basin, and the Ross Sea having the lowest (Figure 10). The $\delta^{13}\text{C}$ signatures were negatively associated with SRP (L-ratio=9.483, df=17, $p=0.002$) and AI (L-ratio=9.412, df=17,

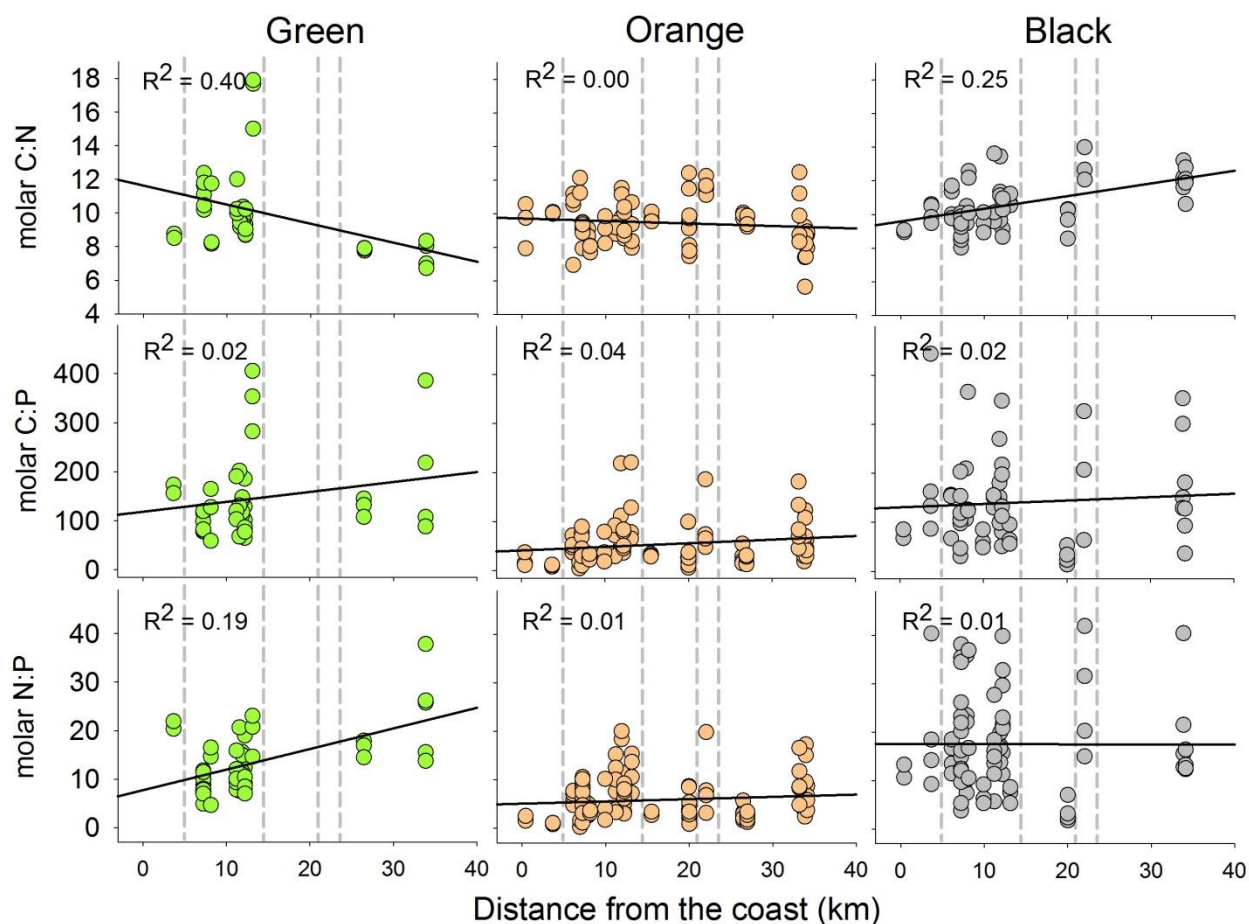


Figure 9: Molar C:N, C:P, and N:P plotted for green (left), orange (middle), and black (right) mats against the distance from the Ross Sea coast. Grey lines separate drainage basins, which from left to right includes the Ross Sea, Lake Fryxell, Lake Hoare, Mummy Pond, and Lake Bonney.

$p=0.002$), but positively correlated with DIN (L-ratio=4.402, $df=17$, $p=0.036$). Green mat $\delta^{15}\text{N}$ signatures were also different by basin (L-ratio=63.492, $df=5$, $p<0.001$), and were higher in Lake Fryxell and lower in Lake Bonney. Finally, green mat $\delta^{15}\text{N}$ was positively associated with SRP (L-ratio=14.383, $df=6$, $p<0.001$).

Orange mats (Table 3) exhibited significantly different C:N ratios by drainage basin (L-ratio = 42.190, $df = 25$, $p < 0.001$), with greatest values coming from stream samples draining into Mummy Pond and the Ross Sea, and the lowest values from streams draining into Lake

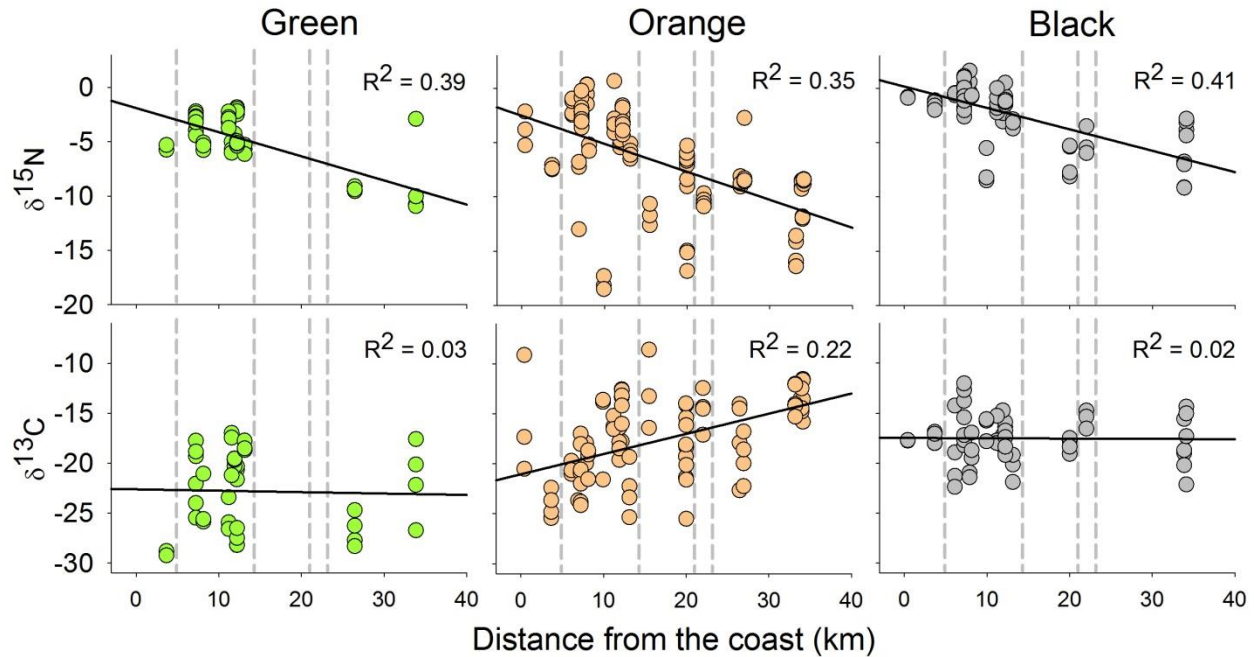


Figure 10: $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ plotted for green (left), orange (middle), and black (right) mats against the distance from the Ross Sea coast. Grey lines separate drainage basins, which from left to right includes the Ross Sea, Lake Fryxell, Lake Hoare, Mummy Pond, and Lake Bonney.

Bonney (Figure 9). Neither nutrient concentrations nor AI were included in the minimum adequate models for orange mat C:N. Orange mat C:P (L-ratio=-94.43978, df=8, $p<0.001$) and N:P (L-ratio=47.213, df=8, $p<0.001$) ratios were also different by lake basin, with lowest values for both found in streams draining into the Ross Sea, and highest values in Mummy Pond. Both orange mat C:P (L-ratio=12.141, df=11, $p=0.001$) and N:P (L-ratio=12.371, df=11, $p<0.001$) were significantly reduced by increasing SRP concentrations. Furthermore, both C:P (L-ratio=7.793, df=11, $p=0.005$) and N:P (L-ratio=10.960, df=11, $p=0.001$) ratios were positively related to AI. The $\delta^{13}\text{C}$ (L-ratio=28.520, df=2, $p<0.001$) and $\delta^{15}\text{N}$ (L-ratio=62.190, df=30, $p<0.001$) signatures of orange mats were strongly influenced by basin of origin (Figure 10). However, while $\delta^{13}\text{C}$ increased from the Ross Sea to the Bonney Basin, $\delta^{15}\text{N}$ decreased over the same interval. Furthermore, the minimum adequate model in describing orange mat $\delta^{15}\text{N}$ included a negative relationship with DIN (L-ratio=7.981, df=33, $p=0.005$) and AI (L-ratio=7.32967, df=33,

Table 3: Minimum adequate general least squares (GLS) model output describing orange mat characteristics. Abbreviations are as follows: df = degrees of freedom, loglike = log-likelihood, vf = variance function, SRP = soluble reactive phosphorus, DIN = dissolved inorganic nitrogen, DOC = dissolved organic carbon, and AI = autotrophic index.

Mat type	Variable	df	loglike	vf	Coefficients	Value	SE	t-value	p-value
Orange	C:N	29	101.888	~1 Stream	(Intercept)	2.286	0.007	305.976	0.000
					Basin(Fryxell)	-0.064	0.012	-5.238	0.000
					Basin(Hoare)	-0.011	0.018	-0.614	0.541
					Basin(Mummy)	0.166	0.029	5.719	0.000
					Basin(Ross)	0.022	0.008	2.797	0.006
	C:P	12	-76.639	~1 Basin	(Intercept)	6.865	0.786	8.729	0.000
					Basin(Fryxell)	0.114	0.188	0.606	0.546
					Basin(Hoare)	-0.883	0.278	-3.181	0.002
					Basin(Mummy)	-0.235	0.249	-0.942	0.349
					Basin(Ross)	-1.113	0.198	-5.624	0.000
					SRP	-1.027	0.264	-3.885	0.000
					AI	0.214	0.068	3.168	0.002
	N:P	12	-72.607	~1 Basin	(Intercept)	3.928	0.565	6.956	0.000
					(Basin)Fryxell	0.174	0.134	1.299	0.197
					(Basin)Hoare	-0.609	0.172	-3.543	0.001
					(Basin)Mummy	-0.262	0.257	-1.020	0.310
					(Basin)Ross	-0.786	0.139	-5.639	0.000
					SRP	-0.735	0.190	-3.857	0.000
					AI	0.109	0.030	3.691	0.000
	$\delta^{13}\text{C}$	6	-234.5796	none	(Intercept)	-15.107	0.689	-21.936	0.000
					(Basin)Fryxell	-3.279	0.853	-3.846	0.000
					(Basin)Hoare	-2.184	1.135	-1.925	0.058
					(Basin)Mummy	-0.197	2.066	-0.095	0.924
					(Basin)Ross	-8.967	1.822	-4.921	0.000
	$\delta^{15}\text{N}$	34	121.249	~1 Stream	(Intercept)	-3.062	0.040	-77.123	0.000
					(Basin)Fryxell	0.168	0.021	7.912	0.000
					(Basin)Hoare	0.158	0.019	8.332	0.000
					(Basin)Mummy	-0.160	0.021	-7.497	0.000
					(Basin)Ross	-0.094	0.020	-4.777	0.000
					SRP	0.160	0.015	10.836	0.000
					DIN	-0.034	0.005	-7.222	0.000
					DOC	0.071	0.011	6.467	0.000
					AI	-0.011	0.003	-4.137	0.000

p=0.007), and a positive relationship with DOC (L-ratio=10.77571, df=33, p=0.001) and SRP (L-ratio=8.753, df=33, p=0.003).

When minimum adequate models were made for black mats (Table 4), C:N ratios significantly differed by drainage basin (L-ratio=21.371, df=4, p<0.001), with highest values from Mummy Pond and Lake Bonney, and lowest values from Lake Fryxell and Hoare (Figure

Table 4: Minimum adequate general least squares (GLS) model output describing black mat characteristics. Abbreviations are as follows: df = degrees of freedom, loglike = log-likelihood, vf = variance function, SRP = soluble reactive phosphorus, DIN = dissolved inorganic nitrogen, DOC = dissolved organic carbon, and AI = autotrophic index.

Mat type	Variable	df	loglike	vf	Coefficients	Value	SE	t-value	p-value
Black	C:N	8	61.376	none	(Intercept)	2.617	0.114	22.918	0.000
					Basin(Fryxell)	-0.205	0.060	-3.433	0.001
					Basin(Hoare)	-0.236	0.074	-3.192	0.002
					Basin(Mummy)	-0.026	0.085	-0.308	0.759
					Basin(Ross)	-0.208	0.073	-2.855	0.006
					DIN	-0.033	0.016	-2.021	0.048
					AI	-0.072	0.026	-2.795	0.007
	C:P	7	-51.791	none	(Intercept)	6.640	0.615	10.799	0.000
					Basin(Fryxell)	-0.818	0.319	-2.559	0.013
					Basin(Hoare)	-2.222	0.410	-5.419	0.000
					Basin(Mummy)	-0.756	0.498	-1.517	0.135
					Basin(Ross)	-0.433	0.413	-1.049	0.299
					DIN	-0.274	0.094	-2.906	0.005
	N:P	7	-56.328	none	(Intercept)	4.299	0.469	9.175	0.000
					Basin(Fryxell)	-0.746	0.272	-2.745	0.008
					Basin(Hoare)	-2.192	0.353	-6.218	0.000
					Basin(Mummy)	-0.375	0.391	-0.957	0.342
					Basin(Ross)	-0.480	0.354	-1.354	0.180
					DIN	-0.242	0.070	-3.450	0.001
	$\delta^{13}\text{C}$	22	-109.989	~1 Stream	(Intercept)	-20.019	1.108	-18.064	0.000
					Basin(Fryxell)	1.458	0.927	1.573	0.122
					Basin(Hoare)	-1.050	0.931	-1.129	0.264
					Basin(Mummy)	3.647	1.082	3.372	0.001
					Basin(Ross)	0.964	0.855	1.127	0.265
					DOC	-1.393	0.455	-3.062	0.003
					AI	0.541	0.219	2.473	0.017
	$\delta^{15}\text{N}$	22	21.938	~1 Stream	(Intercept)	-1.394	0.075	-18.529	0.000
					Basin(Fryxell)	0.174	0.069	2.533	0.014
					Basin(Hoare)	-0.392	0.095	-4.144	0.000
					Basin(Mummy)	-0.507	0.099	-5.142	0.000
					Basin(Ross)	0.173	0.072	2.403	0.019
					DOC	0.215	0.023	9.169	0.000

9). Black C:N ratios were reduced by increasing DIN concentrations (L-ratio=4.433 df=7, p=0.035) and AI values (L-ratio=8.225, df=7, p=0.004). The C:P (L-ratio=29.444, df=3, p<0.001) and N:P (L-ratio=38.230, df=3, p<0.001) ratios of black mats were highest in the Ross Sea and Mummy Pond basins, but lowest in streams draining into Lake Hoare. Both C:P (L-ratio=8.702, df=6, p=0.003) and N:P (L-ratio=11.932, df=6, p=0.001) ratios were negatively

related to DIN. Both the $\delta^{13}\text{C}$ (L-ratio=16.888, d=18, p=0.002) and $\delta^{15}\text{N}$ (L-ratio=27.946, df=18, p<0.001) signatures were dependent upon drainage basin (Figure 10). Black mat $\delta^{15}\text{N}$ was highest in basins near the coast, and declined towards the west, while $\delta^{13}\text{C}$ was more similar among basins with the exception of Mummy pond, which had high values (Figure 10). The $\delta^{13}\text{C}$ signatures were negatively related to DOC (L-ratio=8.203, df=21, p=0.004), but positively related to AI (L-ratio=5.355, df=21, p=0.021). Finally, black mat $\delta^{15}\text{N}$ signatures were positively correlated with DOC (L-ratio=30.002, df=21, p<0.001).

DISCUSSION

Mat type, ambient nutrient concentration, and longitudinal location within streams are important considerations to the elemental and isotopic composition of MDV microbial mats. Orange and green mats residing within the stream channel were the most influenced by dissolved P concentrations, reflecting widespread limitation of P throughout Taylor Valley as suggested by dissolved N:P ratios in the water column. However black mats, which reside on the stream margins, were little affected by SRP, and were instead consistently correlated with DIN. The $\delta^{15}\text{N}$ signature of all mat types was strongly related to the distance from the coast and the longitudinal location within the stream, with mat communities becoming more enriched as nitrogen becomes less available and the role of N-fixation more important, though more depleted in areas with greater accumulated NO_3^- deposition. These results will benefit investigators using isotopes and nutrient stoichiometry as ecological tools by helping to understand sources of heterogeneity in basal resources, which is reflected in higher trophic levels (Zah et al. 2001, Dodds et al. 2014).

Stoichiometry

Different mat types were distinct in their stoichiometric composition, and results were directly related to mat structure. The high %C of black mats is likely due to the mucilaginous sheath produced by *Nostoc*, which is a large part of the colony by volume and comprised of extrapolsaccharides (Potts 2000). Chlorophyte-based green mats have the most Chl-a relative to AFDM, and the high N density of Chl-a (4 N atoms per molecule) helps explain their high N content. Contrary to Rochera et al. (2013), who found orange mats to have high C:P ratios, we found orange mats overall to be enriched in P compared to other mat types. Interestingly, while there was much observed variability in these mat nutrient ratios, relationships with nutrients were specific to individual mat types.

Algae are able to assimilate excess nutrients when they become available (Sternner and Elser 2002), and cyanobacteria specifically are able to store excess N and P within extracellular polymeric substances such as cyanophycin or polyphosphate bodies, respectively (Dodds et al. 1995, Stal 2000). Therefore, it is interesting to note the weak relationship between orange and green mat stoichiometry to DIN. One reason for this may be in the relatively high N:P ratios of the water column, which may result in a general limitation in P. If this is the case, we might expect responses to changes in SRP, but not DIN. In our study, orange and green mat N:P and orange mat C:P ratios were significantly reduced by increases in SRP, which indicates P storage for these mats.

Interestingly, the C:N:P stoichiometry of black mats was significantly associated with DIN, which is surprising given the marginal position of mats which minimizes exposure to stream water, the overall high N:P ratios in Taylor Valley, and the assumption that black mats should be liberated from N-limitation due to the ability of *Nostoc* to fix N₂ from the atmosphere.

One possibility is in the mechanism outlined in Otero and Vincenzini (2004), whereby when *Nostoc* C-fixation exceeds N-fixation, or when N-limited in general, the production of C-rich exopolysaccharides is elevated. Therefore, decreases in N availability could drive up the C:N or C:P ratios in black mats, which is consistent with our observations. Furthermore, the negative relationship with DIN and N:P may be the result of “coupled uptake”, where the availability of one nutrient (especially the limiting one) may facilitate attaining another (eg. Schade et al. 2011).

Habitat use may also help explain stoichiometric ratios, as Davey (1993) previously found Maritime Antarctic mats have different stoichiometries depending on where they are found in the stream (margin vs. channel). The lower C:N:P ratios of green and orange mats may be related to their greater exposure to flow, which increases nutrient delivery and availability (Biggs et al. 1998). The high P content of orange mats specifically may be due to their proximity to the hyporheic zone where weathering takes place (Maurice et al. 2002). Similarly, the weak relationship between P content and SRP concentration for black mats may be a result of their being outside the streambed.

$\delta^{15}\text{N}$

We found the $\delta^{15}\text{N}$ of mats to be relatively depleted overall, distinct by mat type, and to exhibit a much greater range of values than in previous reports (Burkins et al. 2000, Lawson et al. 2004, Hage et al. 2007). As predicted, black mat $\delta^{15}\text{N}$ signatures were the most enriched and near the atmospheric standard reflecting N-fixation (Peterson and Fry 1987, Michener and Lajtha 2007), while green and orange mats were more variable and depleted than black mats. Since they cannot fix N, these latter mat types may be more prone to environmental variability, and should be more enriched where nitrogen is more scarce. This hypothesis was supported by the observation of all

mat type $\delta^{15}\text{N}$ signatures becoming more enriched towards the coast where lower concentrations of DIN have been historically measured by the MCMLTER (Welch et al. 2010), and has previously been demonstrated for periphyton over a nitrate gradient in Brabandere et al. (2007). This reflects the preferential removal of the lighter isotope from the water column through biological activity (Montoya and McCarthy 1995), and perhaps a greater degree of recycling (shorter spiral lengths) of materials such as ammonia and amino acids where biomass is high and DIN low.

Fixation from abundant black mats may be responsible for “new nitrogen” in nutrient depleted streams, and the high biomass of *Nostoc* may even be necessary to sustain microbial mat biomass throughout the Fryxell basin where N is low. Evidence for the facilitation of mat biomass by *Nostoc* mats can be visualized in the longitudinal $\delta^{15}\text{N}$ signatures within the Relict Channel. Here, orange mat $\delta^{15}\text{N}$ quickly become enriched downstream to match the isotopic signature of black mats, though not becoming more enriched than black mats, which might happen if nitrogen was to continue to be recycled and no new nitrogen was entering the system. Furthermore, the Harnish Creek Gage with high upstream black mat biomass had much more enriched mat $\delta^{15}\text{N}$ signatures than the neighboring VG Stream Gage, which has much lower black mat biomass. As a result, it is possible that this N is derived from black mats, and *Nostoc* have previously been shown to provide substantial nitrogen inputs to MDV streams (Howard-Williams et al. 1989, McKnight et al. 2007), Antarctic mosses (Christie 1987), and other ecosystems globally (reviewed by Dodds et al. 1995).

The upstream/downstream comparisons are consistent with nitrogen being recycled to a greater extent in the downstream direction regardless of fixation by *Nostoc*. Processes such as nitrification and denitrification have large effects on N isotopes (Lehmann et al 2003, Michener

and Lajtha 2007), and increases in signature may indicate greater levels of nitrogen cycling in streams. The lone exception to this is the Onyx River, which flows almost 30 km inland before it empties into Lake Vanda, and has little or no *Nostoc*. Here, orange mats were much more depleted in $\delta^{15}\text{N}$ than Lake Brownworth counterparts. Previous studies have shown that nutrient concentrations increase from Lake Brownworth until a few km from Lake Vanda (Howard-Williams et al. 1997, Green et al. 2005), presumably due to the input of many small, low biomass tributaries. However, before reaching Lake Vanda, nutrient concentrations sharply decline near an area called the “Boulder Pavement” (Howard-Williams et al. 1997, Green et al. 2005), which is a designated Scientific Zone with high mat density, and is probably responsible for the sharp reduction in dissolved nutrient concentrations. We found the Lake Vanda inlet to have greater DIN than Lake Brownworth on average in our comparison, and can therefore assume that these tributaries provide enough depleted N deposited from the atmosphere to alter mat signatures in the opposite direction we would hypothesize.

While *Nostoc* are certainly fixing N, they may also exhibit N-uptake (Dodds et al. 1995), as suggested by $\delta^{15}\text{N}$ signatures. In both the stoichiometry and isotope data, black mats are sometimes strictly homeostatic (ie. Relict $\delta^{15}\text{N}$), but other times are highly correlated with available nutrients or the distance from the coast (ie. more depleted in $\delta^{15}\text{N}$ with high DIN), indicating nutrients derived from the water column rather than the atmosphere. An example is the highly depleted $\delta^{15}\text{N}$ signatures of Huey Creek orange and black mats in the Fryxell basin. Huey drains a snowfield originating in the Asgard Range, and the sparse mats here are restricted to lateral branches, likely due to frequent flooding and unstable substrata (Runkel et al. 1998, Koch et al. 2010). These characteristics allow long N spiral lengths, and thus more depleted $\delta^{15}\text{N}$ signatures. While not unusual for orange mats, black mats are also highly depleted here, as well

as in up-valley sites like Lawson. Hyporheic streamwater, the use of which by black mats is corroborated by temperature and moisture data (Stanish, *unpublished*), is variable with streamflow and in regeneration time. Therefore the ability to alternate nutrient pathways may be valuable, depending on distance from the stream margin, immersion frequency, and DIN availability.

$\delta^{13}\text{C}$

Mat types were also different in their $\delta^{13}\text{C}$ ratios, and were within the range of previously reported values (Doran et al. 1998, Lawson et al. 2004, Hage et al. 2007). Like for other analytes, differences were probably due to the composition of dominant taxonomic constituents. For example, the exopolymeric substances that comprise the sheaths of filamentous cyanobacteria have been shown to be more enriched in $\delta^{13}\text{C}$ than the bulk cell material (van Dongen et al. 2002). Furthermore, carbon concentrating mechanisms present in this group may furthermore lead to enriched signatures (ex. Badger et al. 2002, Hanson et al. 2014). Therefore, since orange, black, and red mats are primarily cyanobacterial, it follows that they would exhibit greater $\delta^{13}\text{C}$ signatures than green algal mats (ex. Rochera et al. 2013). Similarly, eukaryotic phytoplankton (i.e. diatoms, chrysophytes, and chlorophytes) have been previously shown to be more depleted than their cyanobacterial counterparts (Vuorio et al. 2006), perhaps due to systematic differences in fractionation.

Differences were also likely a product of mat habitat. Like for nutrients, primary producer $\delta^{13}\text{C}$ signatures may be influenced by the size of the boundary layer surrounding cells, which controls the diffusion rate of CO_2 (Keeley and Sandquist 1992, Des Marais and Canfield 1994). Therefore, high velocity streams with more atmospheric exchange may produce

comparatively depleted mat $\delta^{13}\text{C}$ signatures (Finlay et al. 1999, Finlay and Kendall 2007), while factors increasing biomass or slowing water velocities create CO_2 limitation, enriching signatures (Laws et al. 1995, Schouten et al. 2001, Hill et al. 2008). Like in Rochera et al. (2013), our data show that green mats are far more depleted in $\delta^{13}\text{C}$ than other mats types, which may be a function of their streamer-like morphology. This is in contrast to orange mats, which often occupy seep or wetland areas where green mats are absent, and where C diffusion is slower.

Variation in signature may also arise from the alternation between HCO_3^- and CO_2 as a carbon source, and mats may be more able to isotopically discriminate CO_2 than DIC (Des Marais and Canfield 1994). Therefore, when CO_2 is limiting, the isotopic signature of DIC may have a large influence on mat $\delta^{13}\text{C}$ signatures (Des Marais and Canfield 1994, Finlay et al. 2004). The MDVs have some of the highest $\delta^{13}\text{C}$ values for DIC ever reported for streams, and Wormherder Creek specifically has some of the highest reported values (~ 5 , Lyons et al. 2013). It comes as no surprise then that these high values are also reflected in the Wormherder microbial mat $\delta^{13}\text{C}$ signatures, and orange mats in general became more enriched in $\delta^{13}\text{C}$ away from the coast. However, the opposite pattern was observed in the Onyx River, where orange mat $\delta^{13}\text{C}$ signatures were much more depleted at the Lake Vanda site compared to Lake Brownworth, which is opposite the trend in DIC shown in Lyons et al. (2013), and may suggest an alternative carbon source for these mats.

Future directions and conclusions

The elemental signatures of stream primary producers are relatively difficult to predict due to habitat and trophic complexity. In this study, which utilized a simplified stream system, both the taxonomic identity and distance from the coast proved to be valuable in predicting the elemental

content of microbial mats. Furthermore, individual streams and basins were among the most useful variables, which should be self-evident as individual water bodies have their own histories, trajectories, and fates. In particular, the level of whole-stream biomass, hyporheic storage, and wetland area may be helpful in describing much of our unaccounted for variability. However, relationships with specific variables such as DIN and SRP were not as straightforward as have been demonstrated in other, more trophically complex systems, and warrants further investigation.

Observed variability may also be explained at smaller scales, and related to inherent habitat heterogeneity within reaches. For example, McKnight et al. (2004) found that water chemistry within VG Stream significantly differed between the source glacier, water column, seeps, and the hyporheic zone. Furthermore, stoichiometric ratios have previously been shown to be sensitive to interannual variation in flow (Chapter II), adding yet another layer of complexity. Nutrient diffusing substrata and microhabitat sampling, along with the analyses of exopolymeric substances (Rochera et al. 2013), lipid biomarkers (Hage et al. 2007), and extracellular enzymes activity (Hill et al. 2012) may help distinguish in-stream processes and connect results with nutrient concentrations of mats and streamwater.

The future climate of Polar Regions is predicted to change, and the MDVs are expected to warm in coming decades (Walsh, 2009). With increased glacial melt, the flow regime of streams is projected to change markedly (Gooseff et al. 2011), and may be accompanied by a change in nutrient status (Rouse et al. 1997, Hobbie et al. 1999, Quayle et al. 2002, Walvoord and Striegl 2007), leading to alterations in biogeochemical cycling and changes in stream morphology (Levy et al. 2013, Fountain et al. 2014). Microbial mat abundance and composition are likely to follow suit (Chapter III), altering the amount and type of nutrients reaching the

closed-basin lake ecosystems, as well as that locked in biomass. Understanding how microbial communities store and cycle these nutrients will aid in helping us understanding their ecology, but ultimately the future of ecosystems like the MDVs, which represent some of the most rapidly changing parts of the planet.

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REFERENCES

- Abe, S.I., Sakano, H., Kobayashi, S., and Kitano, S. 2014. Stable carbon isotope variability associated with taxonomic composition of lotic benthic algae. *Phycological Research* 62(1): 73-76.
- Alger, A.S., McKnight, D.M., Spaulding, S.A., Tate, C.M., Shupe, G.H., Welch, K.A., Edwards, R., Andrews, E.D., and House, H.R. 1997. Ecological processes in a cold desert ecosystem: the abundance and species distribution of algal mats in glacial meltwater streams in Taylor Valley, Antarctica. *Institute of Arctic and Alpine Research Occasional Paper*, 51.
- Badger, M.R., Hanson, D., and Price, G.D. 2002. Evolution and diversity of CO₂ concentrating mechanisms in cyanobacteria. *Functional Plant Biology* 29(3): 161-173.
- Ball, B.A., and R.A. Virginia. 2014. The ecological role of moss in a polar desert: implications for aboveground–belowground and terrestrial–aquatic linkages. *Polar Biology* 37: 651–664. doi: 10.1007/s00300-014-1465-2
- Barrett, J.E., Virginia, R.A., Hopkins, D.W., Aislabie, J., Bargagli, R., Bockheim, J.G, Campbell, I.B., Lyons, W.B., Moorhead, D.L., Nkem, J.N., Sletten, R.S., Steltzer, H., Wall, D.H., and

- Wallenstein, M.D. 2006. Terrestrial ecosystem processes of Victoria Land, Antarctica. *Soil Biology and Biogeochemistry* 38: 3019-3034. doi: 10.1016/j.soilbio.2006.04.041
- Barrett, J.E., Virginia, R.A., Lyons, W.B., McKnight, D.M., Priscu, J.C., Doran, P.T., Fountain, A.G., Wall, D.H., and Moorhead, D.L. 2007. Biogeochemical stoichiometry of Antarctic Dry Valley ecosystems. *Journal of Geophysical Research* 112: G01010. doi: 10.1029/2005JG000141
- Bate, D.B., Barrett, J.E., Poage, M.A., and Virginia, R.A. 2008. Soil phosphorus cycling in an Antarctic polar desert. *Geoderma* 144(1): 21-31. doi:10.1016/j.geoderma.2007.10.007
- Bates, D., Maechler, M., Bolker, B. and Walker, S. 2014. lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-7. Available: <http://CRAN.R-project.org/package=lme4>
- Brabandere, L.D., Frazer, T.K. and Montoya, J.P. 2007. Stable nitrogen isotope ratios of macrophytes and associated periphyton along a nitrate gradient in two subtropical, spring-fed streams. *Freshwater Biology* 52: 1564–1575. doi: 10.1111/j.1365-2427.2007.01788.x
- Burkins, M.B., Virginia, R.A., Chamberlain, C.P., and Wall, D.H. 2000. Origin and distribution of soil organic matter in Taylor Valley, Antarctica. *Ecology* 81(9): 2377-2391. doi: 10.1890/0012-9658(2000)081[2377:OADOSO]2.0.CO;2
- Christie, P. 1987. Nitrogen in two contrasting Antarctic bryophyte communities. *Journal of Ecology* 75: 73-93.
- Davey, M.C. 1993. Carbon and nitrogen dynamics in a maritime Antarctic stream. *Freshwater Biology* 30: 319–330.
- Des Marais, D.J., and Canfield, D.E. 1994. The carbon isotope biogeochemistry of microbial mats. In Stal, J., and Caumette, P., Eds. *Microbial mats: structure, development, and environmental significance*. NATO-ASI series, VG35. Berlin Heidelberg: Springer-Verlag, 289–298. doi: 10.1007/978-3-642-78991-5_30
- Dodds, W.K., Collins, S.M., Hamilton, S.K., Tank, J.L., Johnson, S., Webster, J.R., Simon, K.S., Whiles, M.R., Rantala, H.M., McDowell, W.H., Peterson, S.D., Riis, T., Crenshaw, C.L., Thomas, S.A., Kristensen, P.B., Cheever, B.M., Flecker, A.S., Griffiths, N.A., Cowl, T., Rosi-Marshall, E.J., El-Sabaawi, R., and Martí, E. 2014. You are not always what we think you eat: selective assimilation across multiple whole-stream isotopic tracer studies. *Ecology* 95(10): 2757-2767.
- Dodds, W.K., Gudder, D.A., and Mollenhauer, D. 1995. The ecology of Nostoc. *Journal of Phycology* 31: 2-18. doi: 10.1111/j.0022-3646.1995.00002.x
- Finlay, J.C. 2004. Patterns and controls of lotic algal stable carbon isotope ratios. *Limnology and Oceanography* 49: 850–61.

- Finlay, J.C., and Kendall, C. 2007. Stable isotope tracing of temporal and spatial variability in organic matter sources to freshwater ecosystems, In Michener, R., and Lajtha, K., Eds. *Stable isotopes in ecology and environmental science*, 2nd ed. Oxford, UK: Blackwell Publishing, 283-333.
- Finlay, J.C., Power, M.E., and Cabana, G. 1999. Effects of water velocity on algal carbon isotope ratios: Implications for river food web studies. *Limnology and Oceanography* 44: 1198-1203.
- Foreman, C.M., Wolf, C.F., and Priscu, J.C. 2004. Impact of episodic warming events on the physical, chemical, and biological relationships of lakes in the McMurdo Dry Valleys, Antarctica. *Aquatic Geochemistry* 10: 239-268.
- Fountain, A.G., Levy, J.S., Gooseff, M.N., and Van Horn, D. 2014. The McMurdo Dry Valleys: a landscape on the threshold of change. *Geomorphology* 225: 25-35. doi:10.1016/j.geomorph.2014.03.044
- Fountain, A.G., Lyons, W.B., Burkins, M.B., Dana, G.L., Doran, P.T., Lewis, K.J., McKnight, D.M., Moorhead, D.L., Parsons, A.N., Priscu, J.C., Wall, D.H., Wharton, R.A., and Virginia, R.A. 1999. Physical controls on the Taylor Valley ecosystem, Antarctica. *Bioscience* 49: 961-971.
- Gooseff, M.N., Barrett, J.E., and Levy, J.S. 2013. Shallow groundwater systems in a polar desert, McMurdo Dry Valleys, Antarctica. *Hydrogeology Journal* 21: 171-183. doi: 10.1007/s10040-012-0926-3
- Gooseff, M.N., McKnight, D.M., Doran, P., Fountain, A.G., and Lyons, W.B. 2011. Hydrological connectivity of the landscape of the McMurdo Dry Valleys, Antarctica. *Geography Compass* 5/9: 666-681. doi: 10.1111/j.1749-8198.2011.00445.x
- Gooseff, M.N., McKnight, D.M., Lyons, W.B., and Blum, A.E. 2002. Weathering reactions and hyporheic exchange controls on stream water chemistry in a glacial meltwater stream in the McMurdo Dry Valleys. *Water Resources Research* 38(12): 15-1.
- Gooseff, M.N., McKnight, D.M., Runkel, R.L., and Duff, J.H. 2004. Denitrification and hydrologic transient storage in a glacial meltwater stream, McMurdo Dry Valleys, Antarctica. *Limnology and Oceanography* 49: 1884-1895.
- Green, W.J., Stage, B.R., Preston, A., Wagers, S., Shacat, J., and Newell, S. 2005. Geochemical processes in the Onyx River, Wright Valley, Antarctica: Major ions, nutrients, trace metals. *Geochimica et Cosmochimica Acta* 69(4): 839-850. doi:10.1016/j.gca.2004.08.001
- Hage, M.M., Uhle, M.E., and Macko, S. 2007. Biomarker and stable isotope characterization of coastal pond-derived organic matter, McMurdo Dry Valleys, Antarctica. *Astrobiology* 7: 645-661. doi: 10.1089/ast.2006.0033

- Hanson, D.T., Collins, A.M., Jones, H.D., Roesgen, J., Lopez-Nieves, S., and Timlin, J.A. 2014. On-line stable isotope gas exchange reveals an inducible but leaky carbon concentrating mechanism in *Nannochloropsis salina*. *Photosynthesis research* 121(2-3): 311-322.
- Hart, D.D., Biggs, B.J.F., Nikora, V.I., and Flinders, C.A. 2013. Flow effects on periphyton patches and their ecological consequences in a New Zealand river. *Freshwater Biology* 58: 1588-1602.
- Hawes, I. 1989. Filamentous green algae in freshwater streams on Signy Island, Antarctica. *Hydrobiologia* 172: 1-18.
- Hedges, J.I., and Stern, J.H. 1984. Carbon and nitrogen determinations of carbonate containing solids. *Limnology and Oceanography* 29: 657-663. doi: 10.4319/lo.1984.29.3.0657
- Hill, B.H., Elonen, C.M., Seifert, L.R., May, A.A., and Tarquinio, E. 2012. Microbial enzyme stoichiometry and nutrient limitation in US streams and rivers. *Ecological Indicators* 18: 540-551.
- Hill, W.R., Fanta, S.E., and Roberts, B.J. 2008. ¹³C dynamics in benthic algae: Effects of light, phosphorus, and biomass development. *Limnology and Oceanography* 53(4): 1217-1226. doi: 10.4319/lo.2008.53.4.1217.
- Hobbie, J.E., Peterson, B.J., Bettez, N., Deegan, L., O'Brien, W.J., Kling, G.W., Kipphut, G.W., Bowden, W.B., and Hershey, A.E. 1999. Impact of global change on the biogeochemistry and ecology of an Arctic freshwater system. *Polar Research* 18: 207-214. doi: 10.1111/j.1751-8369.1999.tb00295.x
- Howard-Williams, C., and Hawes, I. 2007. Ecological processes in Antarctic inland waters: interactions between physical processes and the nitrogen cycle. *Antarctic Science* 19: 205-217. doi: 10.1017/S0954102007000284
- Howard-Williams, C., Hawes, I., Schwarz, A.-M., and Hall, J.A. 1997. Sources and sinks of nutrients in a polar desert stream, the Onyx River, Antarctica. In Lyons, W.B., Howard-Williams, C., and Hawes, I., Eds. *Ecosystem Processes in Antarctic Ice-Free Landscapes*. Rotterdam, Netherlands: Balkema Press, 155-170.
- Howard-Williams, C., Priscu, J.C., and Vincent, W.F. 1989. Nitrogen dynamics in two Antarctic streams. *Hydrobiologia* 172: 51-61.
- Howard-Williams, C., Vincent, C.L., Broady, P.A., and Vincent, W.F. 1986. Antarctic stream ecosystems: Variability in environmental properties and algal community structure. *Internationale Revue der Gesamten Hydrobiologie und Hydrographie* 71: 511-544.
- Keeley, J.E., and Sandquist, D.R. 1992. Carbon: freshwater plants. *Plant, Cell and Environment* 15(9): 1021-1035.

- Koch, J.C., McKnight, D.M., and Baeseman, J.L. 2010. Effect of unsteady flow on nitrate loss in an oligotrophic, glacial meltwater stream, *Journal of Geophysical Research-Biogeosciences*, 115: G01001. doi: 10.1029/2009JG001030
- Kohler, T.J., Heatherly II, T.N., El-Sabaawi, R.W., Zandonà, E., Marshall, M.C., Flecker, A.S., Pringle, C.M., Reznick, D.N., and Thomas, S.A. 2012. Flow, nutrients and light availability influence Neotropical epilithon biomass and stoichiometry. *Freshwater Science* 31: 1019-1034. doi: 10.1899/11-141.1
- Kohler, T.J., Murdock, J.N., Gido, K.B., and Dodds, W.K. 2011. Nutrient loading and grazing by the minnow *Phoxinus erythrogaster* shift periphyton abundance and stoichiometry in mesocosms. *Freshwater Biology* 56: 1133-1146. doi: 10.1111/j.1365-2427.2010.02557.x
- Kuznetsova, A., Brockhoff, P.B., and Christensen, R.H.B. 2014. lmerTest: Tests for random and fixed effects for linear mixed effect models (lmer objects of lme4 package). R package version 2.0-11. Availailbe: <http://CRAN.R-project.org/package=lmerTest>
- Laws, E.A., Popp, B.N., Bidigare, R.R., Kennicutt, M.C., and Macko, S.A. 1995. Dependence of phytoplankton carbon isotopic composition on growth rate and $[CO_2]_{aq}$: Theoretical considerations and experimental results. *Geochimica et Cosmochimica Acta* 59: 1131-1138.
- Lawson, J., Doran, P.T., Kenig, F., Des Marais, D.J., and Priscu, J.C. 2004. Stable carbon and nitrogen isotopic composition of benthic and pelagic organic matter in lakes of the McMurdo Dry Valleys, Antarctica. *Aquatic Geochemistry* 10: 269-301. doi: 10.1007/s10498-004-2262-2
- Lawson Knoepfle, J., Doran, P.T., Kenig, F., Lyons, W.B., and Galchenko, V. 2009. Particulate organic and dissolved inorganic carbon stable isotopic compositions in Taylor Valley lakes, Antarctica: the effect of legacy. *Hydrobiologia* 632: 139-156.
- Lehmann, M.F., Reichert, P., Bernasconi, S.M., Barbieri, A., and McKenzie, J.A. 2003. Modelling nitrogen and oxygen isotope fractionation during denitrification in a lacustrine redox-transition zone. *Geochimica et Cosmochimica Acta* 67(14): 2529-2542.
- Levy, J.S., Fountain, A.G., Dickson, J.L., Head, J.W., Okal, M., Marchant, D.R., and Watters, J. 2013. Accelerated thermokarst formation in the McMurdo Dry Valleys, Antarctica 3: 2269. doi: 10.1038/srep02269
- Lyons, W.B., Leslie, D.L., Harmon, R.S., Neumann, K., Welch, K.A., Bisson, K.M., and McKnight, D.M. 2013. The carbon stable isotope biogeochemistry of streams, Taylor Valley, Antarctica. *Applied Geochemistry* 32: 26-36.
- Maurice, P.A., McKnight, D.M., Gooseff, M.N., Leff, L., and Fulghum, J.E. 2002. Direct observations of aluminosilicate weathering in the hyporheic zone of an Antarctic dry valley stream. *Geochimica et Cosmochimica Acta* 66: 1335-1347.

- McGinnis, L.D., and Jensen, T.E. 1971. Permafrost-hydrogeologic regimen in two ice-free valleys, Antarctica, from electrical depth sounding. *Quaternary Research* 1(3): 389–409. doi:10.1016/0033-5894(71)90073-1
- McIntyre, P.B., Flecker, A.S., Vanni, M.J., Hood, J.M., Taylor, B.W., and Thomas, S.A. 2008. Fish distributions and nutrient cycling in streams: Can fish create biogeochemical hotspots? *Ecology* 89: 2335-2346.
- McKnight, D.M., Alger, A.S., Tate, C.M., Shupe, G., and Spaulding, S. 1998. Longitudinal patterns in algal abundance and species distribution in meltwater streams in Taylor Valley, Southern Victoria Land, Antarctica. In Priscu, J.C., Ed. *Ecosystem Dynamics in a Polar Desert: The McMurdo Dry Valleys, Antarctica*, Antarctic Research Series Vol. 72. Washington, D.C.: American Geophysical Union, 109–127.
- McKnight, D.M., Niyogi, D.K., Alger, A.S., Bomblies, A., Conovitz, P.A., and Tate, C.M. 1999. Dry valley streams in Antarctica: ecosystems waiting for water. *Bioscience* 49: 985-995.
- McKnight, D.M., Runkel, R.L., Tate, C.M., Duff, J.H., and Moorhead, D.L. 2004. Inorganic N and P dynamics of Antarctic glacial meltwater streams as controlled by hyporheic exchange and benthic autotrophic communities. *Journal of the North American Benthological Society* 23: 171-188.
- McKnight, D.M., Tate, C.M., Andrews, E.D., Niyogi, D.K., Cozzetto, K., Welch, K., Lyons, W.B., and Capone, D.G. 2007. Reactivation of a cryptobiotic stream ecosystem in the McMurdo Dry Valleys, Antarctica: A long-term geomorphological experiment. *Geomorphology* 89: 186-204.
- Michalski, G., Bockheim, J.G., Kendall, C., and Thiemens, M. 2005. Isotopic composition of Antarctic Dry Valley nitrate: Implications for NO_y sources and cycling in Antarctica. *Geophysical Research Letters* 32: L13817. doi: 10.1029/2004GL022121.
- Michener, R., and Lajtha, K. 2007. *Stable isotopes in ecology and environmental science*, 2nd ed. Oxford, UK: Blackwell Publishing, 566 pp.
- Montoya, J.P., and McCarthy, J.J. 1995. Isotopic fractionation during nitrate uptake by phytoplankton grown in continuous culture. *Journal of Plankton Research* 17(3): 439-464.
- Morgan-Kiss, R.M., Priscu, J.C., Pocock, T., Gudynaite-Savitch, L., and Huner, N.P.A. 2006. Adaptation and acclimation of photosynthetic microorganisms to permanently cold environments. *Microbiology and Molecular Biology Reviews* 70: 222-252. doi: 10.1128/MMBR.70.1.222–252.2006
- Murphy, J., and Riley, J.P. 1962. A modified single solution method for determination of phosphate in natural waters. *Analytica Chimica Acta* 26: 31-36.

- Needoba, J.A., Waser, N.A., Harrison, P.J., and Calvert, S.E. 2003. Nitrogen isotope fractionation in 12 species of marine phytoplankton during growth on nitrate. *Marine Ecology Progress Series* 255: 81-91.
- Neumann, K., Lyons, W.B., and Des Marais, D.J. 1998. Inorganic carbon-isotope distribution and budget in the Lake Hoare and Fryxell basins, Taylor Valley, Antarctica. *Annals of Glaciology* 27: 685-690.
- Otero, A., and Vincenzini, M. 2004. *Nostoc* (Cyanophyceae) goes nude: extracellular polysaccharides serve as a sink for reducing power under unbalanced C/N metabolism. *Journal of Phycology* 40: 74-81. doi: 10.1046/j.1529-8817.2004.03067.x
- Peipoch, M., Gacia, E., Pastor, A., Ribot, M., Riera, J.Ll., Sabater, F., and Martí, E. 2014. Intrinsic and extrinsic drivers of autotrophic nitrogen cycling in stream ecosystems: Results from a translocation experiment. *Limnology and Oceanography* 59(6): 1973-1986. doi: 10.4319/lo.2014.59.6.1973
- Peterson, B.J., Bahr, M., and Kling, G.W. 1997. A tracer investigation of nitrogen cycling in a pristine tundra river. *Canadian Journal of Fisheries and Aquatic Sciences* 54(10): 2361-2367.
- Peterson, B.J., and Fry, B. 1987. Stable isotopes in ecosystem studies. *Annual Review of Ecology and Systematics* 18: 293-320.
- Pinheiro, J., Bates, D., Debroy, S., and Sarkar, D. 2006. nlme: an R package for fitting and comparing Gaussian linear and nonlinear mixed-effects models. R project for statistical computing, Vienna, Austria. Available: <http://www.stats.bris.ac.uk/R/>
- Potts, M. 2000. *Nostoc*. In Whitton, B.A., and Potts, M., Eds. *The ecology of cyanobacteria: their diversity in time and space*. Dordrecht, Netherlands: Kluwer Academic Press, 465-504.
- Priscu, J.C. 1995. Phytoplankton nutrient deficiency in lakes of the McMurdo Dry Valleys, Antarctica. *Freshwater Biology* 34: 215-227.
- Quayle, W.C., Peck, L.S., Peat, H., Ellis-Evans, J.C., and Harrigan, P.R. 2002. Extreme responses to climate change in Antarctic lakes. *Science* 295: 645. doi: 10.1126/science.1064074
- R Core Team. 2014. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>.
- Rochera, C., Fernandez-Valiente, E., Van de Vijver, B., Rico, E., Toro, M., Vincent, W.F., Quesada, A., and Camacho, A. 2013. Community structure and photosynthetic activity of benthic biofilms from a waterfall in the maritime Antarctica. *Polar Biology* 36: 1709-1722. doi: 10.1007/s00300-013-1388-3

- Rouse, W.R., Douglas, M.S.V., Hecky, R.E. Hershey, A.E., Kling, G.W., Lesack, L., Marsh, P., McDonald, M., Nicholson, B.J., Roulet, N.T., and Smol, J.P. 1997. Effects of climate change on the freshwaters of arctic and subarctic North America. *Hydrological Processes* 11: 873–902. doi: 10.1002/(SICI)1099-1085(19970630)11:8<873::AID-HYP510>3.0.CO;2-6
- Runkel, R.L., McKnight, D.M., and Andrews, E.D. 1998. Analysis of transient storage subject to unsteady flow: diel flow variation in an Antarctic stream. *Journal of the North American Benthological Society* 17: 143-154.
- Schade, J.D., MacNeill, K., Thomas, S.A., McNeely, F.C., Welter, J.R., Hood, J., Goodrich, M., Power, M.E., and Finlay, J.C. 2011. The stoichiometry of nitrogen and phosphorus spiraling in heterotrophic and autotrophic streams. *Freshwater Biology* 56: 424-436. doi:10.1111/j.1365-2427.2010.02509.x
- Schouten, S., Hartgers, W., Lopez, J., Grimalt, J., and Damste, J. 2001. A molecular isotopic study of ^{13}C -enriched organic matter in evaporitic deposits: recognition of CO_2 -limited ecosystems. *Organic Geochemistry* 32: 277–286. doi: 10.1016/S0146-6380(00)00177-7
- Stal, L.J. 2000. Cyanobacterial mats and stromatolites. In Whitton, B.A. and Potts, M., Eds. *The ecology of cyanobacteria: their diversity in time and space*. Dordrecht, Netherlands: Kluwer Academic Publisher, 61–120.
- Steinman, A., Lamberti, G.A., and Leavitt, P.R. 1996. Biomass and pigments of benthic algae. In Hauer, F.R., and Lamberti, G.A., Eds. *Methods in stream ecology*. 2nd ed. San Diego, CA: Academic Press, 357-379.
- Sterner, R.W., and Elser, J.J. 2002. *Ecological stoichiometry: the biology of elements from molecules to the biosphere*. Princeton, NJ: Princeton University Press, 439 pp.
- Treonis, A.M., Wall, D.H., and Virginia, R.A. 1999. Invertebrate biodiversity in Antarctic dry valley soils and sediments. *Ecosystems* 2: 482-492. doi: 10.1007/s100219900096
- van Dongen, B.E., Schouten, S., and Sinninghe Damsté, J.S. 2002. Carbon isotope variability in monosaccharides and lipids of aquatic algae and terrestrial plants. *Marine Ecology Progress Series* 232: 83–92.
- Varin, T., Lovejoy, C., Jungblut, A.D., Vincent, W.F., and Corbeil, J. 2010. Metagenomic profiling of Arctic microbial mat communities as nutrient scavenging and recycling systems. *Limnology and Oceanography* 55: 1901-1911. doi:10.4319/lo.2010.55.5.1901
- Vincent, W.F., and Quesada, A. 2012. Cyanobacteria in high latitude lakes, rivers and seas. In Whitton, B.A., Ed. *Ecology of cyanobacteria II: their diversity in space and time*. Dordrecht, Netherlands: Springer Science & Business Media, 371-385.

- Vuorio, K., Meili, M. and Sarvala, J. 2006, Taxon-specific variation in the stable isotopic signatures ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of lake phytoplankton. *Freshwater Biology*, 51: 807–822. doi: 10.1111/j.1365-2427.2006.01529.x
- Walsh, J.E. 2009. A comparison of Arctic and Antarctic climate change, present and future. *Antarctic Science* 21: 179-188. doi: 10.1017/S0954102009001874
- Walvoord, M.A., and Striegl, R.G. 2007. Increased groundwater to stream discharge from permafrost thawing in the Yukon River basin: Potential impacts on lateral export of carbon and nitrogen. *Geophysical Research Letters* 34: L12402. doi:10.1029/2007GL030216
- Welch, K.A., Lyons, W.B., Whisner, C., Gardner, C.B., Gooseff, M.N., McKnight, D.M., and Prisco, J.C. 2010. Spatial variations in the geochemistry of glacial meltwater streams in the Taylor Valley, Antarctica. *Antarctic Science* 22: 662-672. doi:10.1017/S0954102010000702
- Welschmeyer, N.A. 1994. Fluorometric analysis of chlorophyll a in the presence of chlorophyll b and pheopigments, *Limnology and Oceanography* 39: 1985–1992. doi: 10.4319/lo.1994.39.8.1985
- West, B.T., Welch, K.B., and Galecki, A.T. 2006. *Linear mixed models: a practical guide using statistical software*. London, UK: Chapman and Hall/CRC Press.
- Zah, R., Burgherr, P., Bernasconi, S.M., and Uehlinger, U. 2001. Stable isotope analysis of macroinvertebrates and their food sources in a glacier stream. *Freshwater Biology* 46: 871–882. doi: 10.1046/j.1365-2427.2001.00720.x
- Zuur, A.F., Ieno, E.N., and Elphick, C.S. 2010. A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution* 1: 3-14.
- Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., and Smith, G.M. 2009. *Mixed effects models and extensions in ecology with R*. New York, NY: Springer New York, 574 pp.

CHAPTER V

CONCLUSIONS AND FUTURE DIRECTIONS

“Happy families are all alike; every unhappy family is unhappy in its own way.”

-Leo Tolstoy, from *Anna Karenina*

INSIGHTS FROM THIS DISSERTATION

Worldwide, humans have both directly and indirectly modified the flow regimes and nutrient status of Earth's lotic waters, carrying substantial ecological consequences that impact both resident biota and human consumers. While the influence of hydrologic regime has been an area of focus in middle latitudes, far less attention has been directed towards Polar Regions. This is changing, however, since these areas are predicted to be the most heavily impacted by future increasing temperatures. As hydrologic regime is a dominant variable in stream ecology, increases in stream flow as a result of augmented glacial melt, along with associated streambed erosion, substrata scouring, and changes in nutrient availability, are sure to impact the distribution and biomass of resident organisms as well as alter the connectivity between habitats (Gooseff et al. 2011). This reality underscores the need to study the relationships between hydrology and stream biota, especially in underserved areas such as the Antarctic.

Energy flow in streams is conceptually illustrated by the River Continuum Concept (Vannote et al. 1980), and subsequent addendums such as the Flood-Pulse Concept (Junk et al. 1989, Tockner and others 2000), the Serial Discontinuity Concept (Ward and Stanford 1995), and the River Wave Concept (Humphries et al. 2014) have led to an increased understanding of how autochthonous and allochthonous sources interact with flow regime. In McMurdo Dry Valley (MDV) streams, allochthonous energy inputs are negligible, and downstream communities depend on autochthonous material to meet energy budgets. As most stream research has been performed in systems with comparably well-developed riparian areas, the simplicity of

the MDVs provides an opportunity to test predictions made by the above conceptual models under controlled conditions, and a basis for understanding similar Arctic streams (Vincent and Quesada 2012) and low latitude hot desert systems (Zeglin et al. 2011).

In this dissertation, factors regulating autotrophic biomass were investigated to shed light on this component of MDV stream energy budgets. Chapter II demonstrated multiple seasons are needed to regrow microbial mat biomass after a discrete disturbance, though multiple mat variables remained dynamic within summers regardless of scour. These results improve our knowledge of mat vulnerability, and aid in interpreting long-term trends. In Chapter III, the biomass of different microbial mat types was shown to have different responses to hydrologic variables over a span of two decades. Stream geomorphology and in-stream habitat was further shown to expose mats to different hydrologic conditions, influencing their response. This highlights the importance of taxonomic identity and habitat use to modeling temporal whole stream productivity. Lastly, in Chapter IV, different mats had unique stoichiometric and isotopic signatures, and variation therein was explained by dissolved concentrations that vary both up- and down-valley, as well as longitudinally within streams. Results shed light into the future role of mat identity in nutrient cycling and storage, especially in light of fluctuating mat biomasses and thermokarst formation.

This work collectively shows that these distinct ecosystem compartments inherently differ in their composition and response to environmental stresses and stimuli (Figure 1). Furthermore, conclusions from this dissertation emphasize that a holistic ecosystem approach should be utilized in considering their past and future status, and results from this simplified trophic network may suggest the same rationale applies to streams of lower latitudes by extension. Lastly, this research will help better understanding the ecologies, connectivity, and

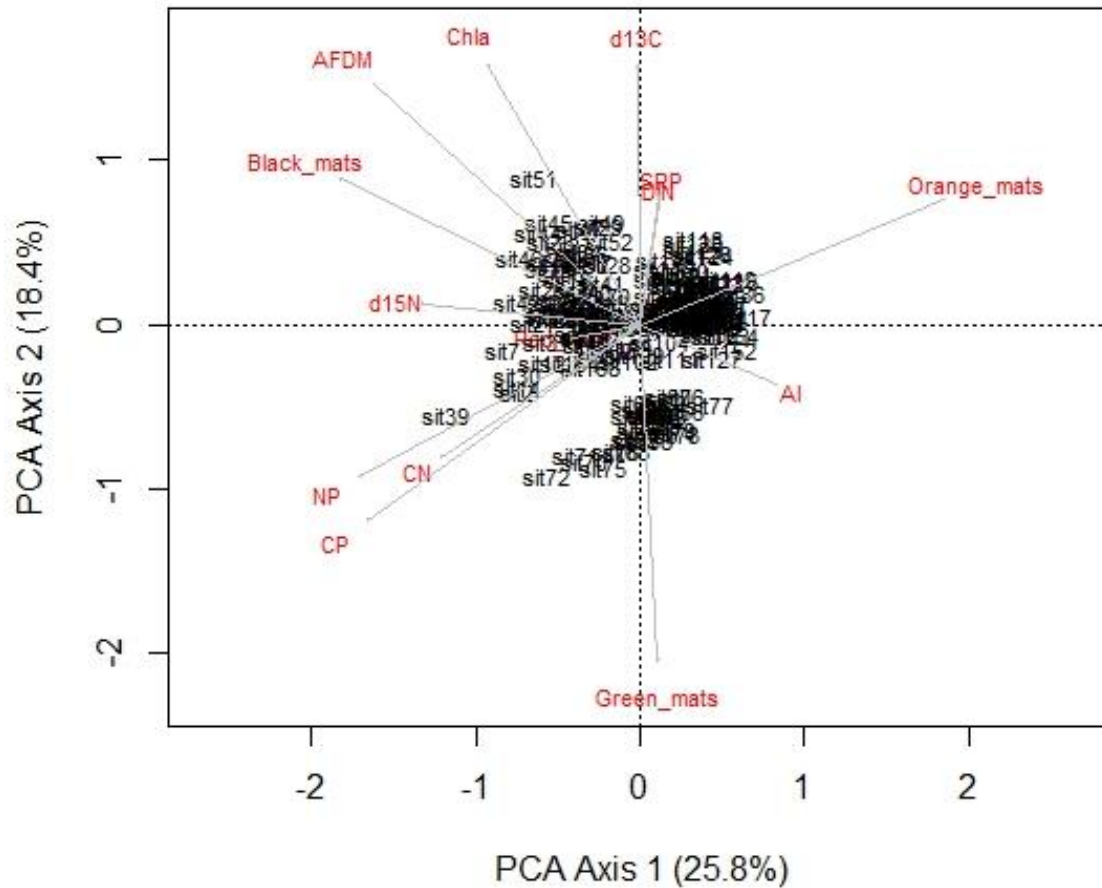


Figure 1: PCA of different biological variables from Chapter IV showing differences between mat types.

mass balance of separate compartments in the MDVs by quantifying elements for redistribution, and can provide insight into the analysis of both past (Wharton et al. 1993) and present organic material (Burkins et al. 2000, Lawson et al. 2004) as well as foodweb structure (Dodds et al. 2004). While this work provides insights into these patterns, plenty of low hanging fruit remain ripe for future investigation in the MDVs, and further directions are highlighted in the subheadings below.

Taxonomy

During the morphological characterization of microbial mat communities in Chapter II, along with differentiating between mat types in Chapters III and IV, it became apparent that further investigation into the identity of the mat component parts is timely. This is especially true for “green mats,” which probably consist of several sub-categories. While often regarded as being comprised of chlorophytes, the very fine green filaments found in streams such as Canada, Green, and Bowles may in fact be cyanobacterial filaments lacking a highly pigmented overstory, and have been identified as such by Alger et al. (1997). Some of these communities may alternatively be comprised of *Microspora* (Kohler, *unpublished*) or contain abundant cryptophytes (Van Horn, *unpublished*). Chlorophyte richness is relatively low in Antarctica (Figure 2), though the genus *Prasiola* (C. Agardh) Meneghini is commonly reported (Izaguirre and Pizarro 1998, Seaburg 1979) and has potential as an environmental indicator in the MDVs (ex. Ohtani et al. 2000). However, *Prasiola* differs considerably in presentation to the finer green mats described above, having much larger, tougher filaments. As a result of these leathery growths, it is more difficult to extract chlorophyll-a from *Prasiola* using current analytical methods (Kohler, *personal observation*).

There is considerable taxonomic uncertainty within *Prasiola* (Broady 1996, Kováčik and Pereira 2001). Molecular work by Moniz et al. (2012) suggests the presence of at least three different Antarctic species, and previous surveys (Fritch 1912, Broady 1996, Vincent and James 1996, Alger et al. 1997) report two species from the McMurdo Sound Region (*P. crispa* (Lightfoot) Kützinger and *P. calophylla* (Carmichael ex Greville) Kützinger), though there is considerable variation and overlap in their descriptions (Kováčik and Pereira 2001). To further complicate matters, *Prasiola* spp have two distinct life stages (Figure 3). The first, called the “Hormidium” stage, is comprised of tough, unbranched, rope-like filaments (West and West

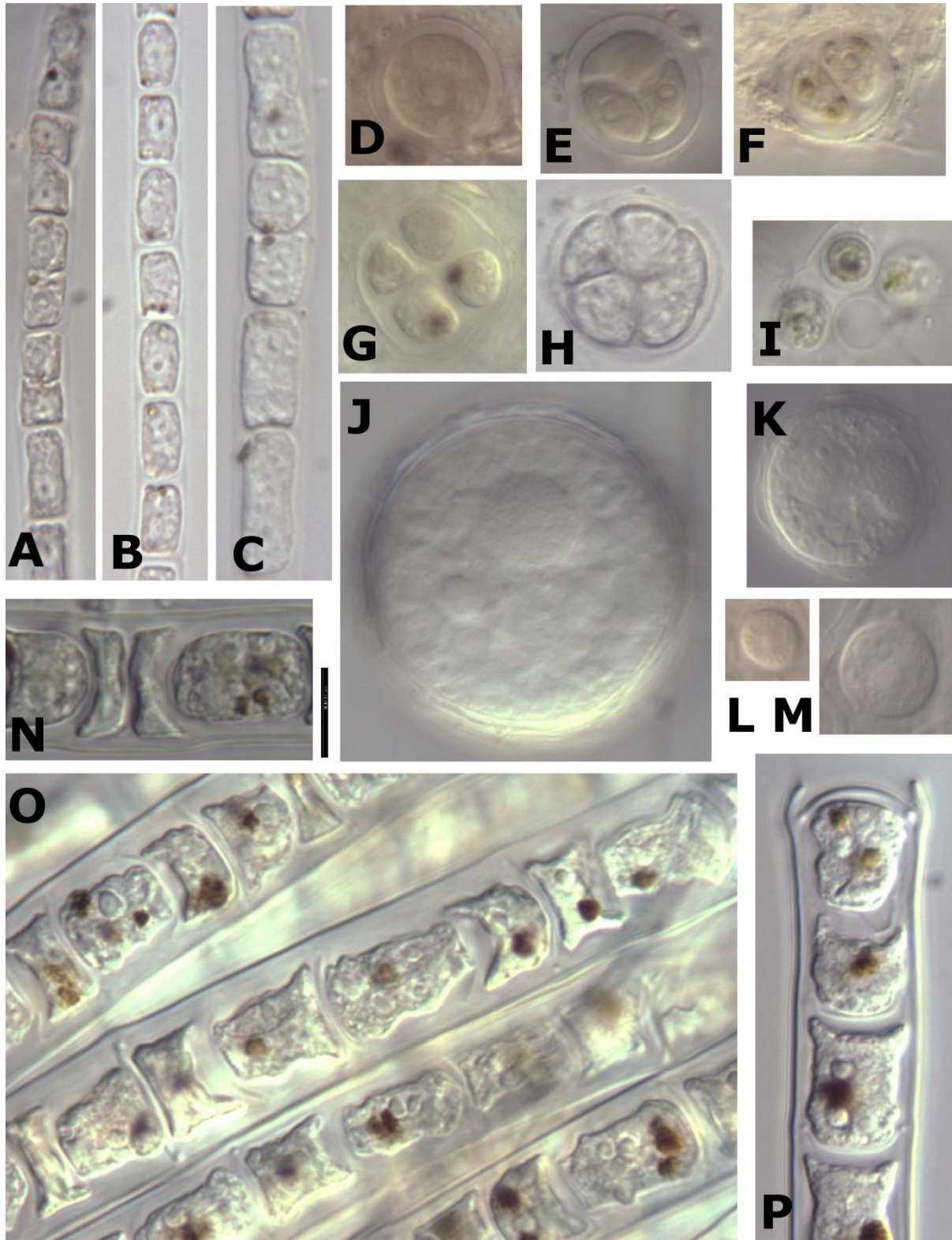


Figure 2: Plate of observed chlorophytes from the McMurdo Sound Region. A-B, *Microspora* filaments from Blue Lake, C, *Zygnema* filament from Blue Lake, D-I, various stages of *Pleurococcus dissectus*, J-K, *Pleurococcus antarcticus*, L-M *Pleurococcus* sp. 1, and N-P, unknown filaments from the shore of Green Lake. Scale bar is 10µm.

1911, West 1927, Seaburg 1979, John 2002, 2003). These are loosely attached to substrata, and reproduction takes place asexually by fragmentation. Hormidium filaments eventually transform into the multiseriate “Schizogonium” stage, characterized by short, thick, multiseriate fronds that form small tufts beneath rocks. At this time, reproduction takes place by aplanospores or oogamy (John 2003), though *Prasiola* sexual cycles are poorly understood (Kováčik and Pereira 2001). Nonetheless, understanding these life cycles are key to interpreting long-term data, as changes in green mat biomass may actually reflect the life history of *Prasiola* rather than a result of physical factors such as streamflow.

The MDV cyanobacteria may be even more problematic (Figure 4), as morphospecies are impossible to differentiate even under ideal preservation due to overlap in morphological descriptions and within-taxon variability. This is especially true for fine trichomes (ex. *Leptolyngbya*, *Pseudoanabeana*, and *Phormidesmis*) which bare virtually no identifiable characteristics aside from their entangled pattern despite modern microscopic methods not available to the pioneering phycologists that described them. These groups have previously been recognized as troublesome (Broady and Kibblewhite 1991, Broady 1996, Komárek 2007, Komárek et al. 2009), although they dominate mat biovolume. Other investigators have coped by focusing on a locality’s trichome morphometrics (Broady and Kibblewhite 1991) or analyzing genera only (Broady 1996). Molecular techniques may be the future for phycologists studying Antarctic cyanobacteria, and recent work already suggests this group to be more diverse than previously assumed (Taton et al. 2003, Taton et al. 2006, Vyverman et al. 2010), making substantial transformations likely in the future (ex. Strunecký et al. 2013).

One widely reported species in Antarctica and elsewhere is *Microcoleus autumnalis* (Trevisan ex Gomont) Strunecký, Komárek & Johansen, which has recently been transferred



Figure 3: Comparison of *Prasiola cf. crista* life stages. A: Field presentation of Hormidium stage in Garwood Stream. B: Field presentation of Schizogonium stage in Commonwealth Stream. C: View of Hormidium filaments under LM. D: View of Schizogonium ribbons under LM from Lawson Creek. E-H: Illustration of the separation of a Hormidium filament. I: Formation of a spore in Hormidium filament. J-K: Separation of uniseriate filament into multiseriate frond. L-N: Detail of Schizogonium frond with the first picture depicting a holdfast. Scalebar is 10µm unless otherwise specified.

from the genus *Phormidium* (Strunecký et al. 2013). This species may represent a taxonomic complex similar to *Luticola muticopsis* (Van Heurck) Mann (See Appendix), in that it is a default category for classification in ecological studies. For example, while West and West (1911) report this species to be common in Pony Lake, the illustrated species does not possess the distinct calyptras and narrowed apical cells typical of the species as described in Fritch (1912) and Komárek and Anagnostidis (2005). While variability is expected, this flexibility may promote confusion with other similar taxa such as *P. formosum*, *P. cortiana*, and *P. terebriforme*, which overlap in their size and morphology. In fact, when I showed the Pony Lake material to Dr. Jiří Komárek in Třeboň, Czech Republic, he suggested that the filament I was positive belonged to *M. autumnalis* was perhaps *Phormidium attenuatus* or even a *Kamptonema* spp. Care is therefore suggested to those interpreting cyanobacterial diversity results and species descriptions based on morphology alone from the literature.

The diatom flora of the MDVs is unique in that the majority of the species are pennate, raphid, and aerophyllic, and total richness is low compared with other habitats worldwide (Figure 5, Table 1). However, many diatoms previously thought to be cosmopolitan are now considered endemic based on new criteria (Vyverman et al. 2007, Vyverman et al. 2010, Souffreau et al. 2013), and many MDV taxa will require revisions based solely on morphology and new observations under SEM. Specifically, the genus *Hantzschia* needs complete revision, and there are several new species of *Chamaepinnularia*, *Microfissurata*, and *Halamphora* that await description. Additionally, some reported species of *Mayamaea*, *Navicula*, and others almost certainly need to be transferred to a different genus. With missing original material, compounded with specimen scarcity, this will be no easy task. Furthermore, molecular efforts are

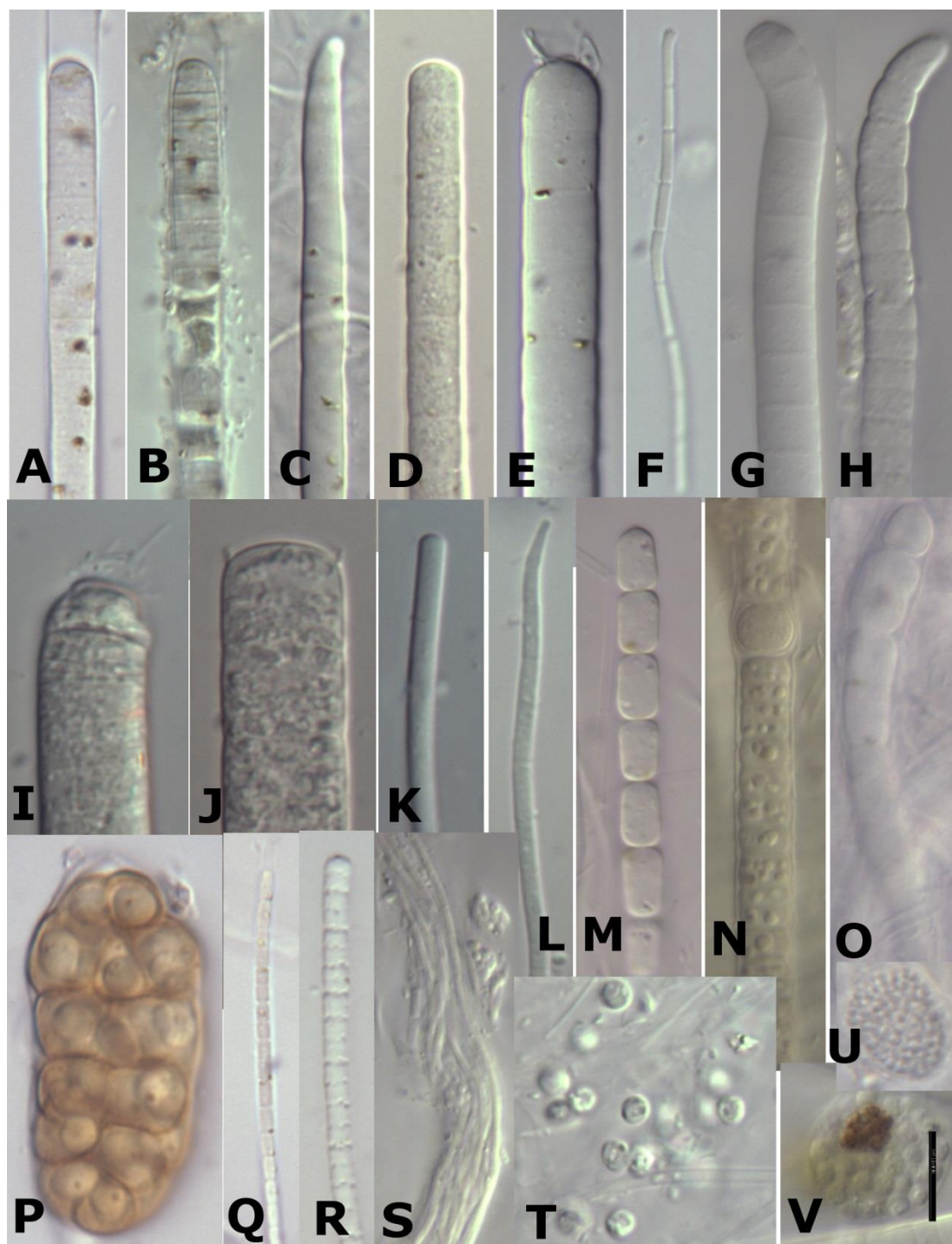


Figure 4: Plate of observed cyanobacteria from the McMurdo Sound Region. A, *Phormidium inundatum*, B, *Lyngbya martensiana*, C, *P. cortianum*, D, *P. terebriformis*, E, *Oscillatoria tenuis*, F, *Planktolyngbya limnetica*, G, *Microcoleus autumnale*, H, *P. pseudopriestlyi*, I, *O. subprobscidea*, J, *O. limosa*, K, *P. chlorinum*, L, *Geitlerinema deflexum*, M, *Pseudoanabaena* sp. 1, N, *Nodularia quadrata*. 1, O, *Calothrix* sp 1, P, *Nostoc* sp. 1, Q, *Leptolyngbya glacialis* or *vincentii*, R, *Wilmottia murrayi*, S, *Leptolyngbya* cf. *fritschiana*, T, *Chroococcus* cf *minor*, U, *Microcystis* sp 1, and V. Unknown coccoids. Scale bar is 10µm.

sorely lacking, and without this information, it may remain unknown how MDV diatoms are different or similar to others locally and worldwide.

Dry Valley diatoms remain mysterious in many ways, and where they spatially reside within mats and what they do there is almost completely unknown. Furthermore, there is still a wealth of environments that have not been analyzed for diatoms at all, some of which are certain to contain undescribed species. For example, diatom species richness increases towards the coast (Stanish et al. 2013), and the stream with the greatest observed species richness (Wales) was not sampled before the 2011-12 summer. The small upland ponds, cryoconites, wetted soils, and mosses have been neglected until recently, although studies elsewhere have found important floral differences between these habitats (Kopalová and Van de Vijver 2013, Kopalová et al. 2013). Mosses in particular represent unique MDV habitats (Ball and Virginia 2014), and have been found to be diverse and distinct from other diatom habitats in Maritime Antarctica (Kopalová et al. 2014). Seal mummies, submerged by rising lake levels, may also be of interest to phycologists due to the dense algal that grows upon them (ex. Nývlt et al., *unpublished*, Figure 6), yet remain a frontier in the MDVs.

Ecology

All three domains of life presumably interact within the MDV mat phycosphere. Although correlations between cyanobacteria and diatoms have been observed (Stanish et al. 2012), current analytical techniques prevent us from disentangling “who is doing what and why” at a fine scale (Stanish and Spear 2013). Of particular interest may be investigating how interactions promote survivability within the matrix, as sometimes external conditions are less than favorable (i.e. picture pond, Sakaeva 2014). Enzymatic and molecular analyses conducted as a function of

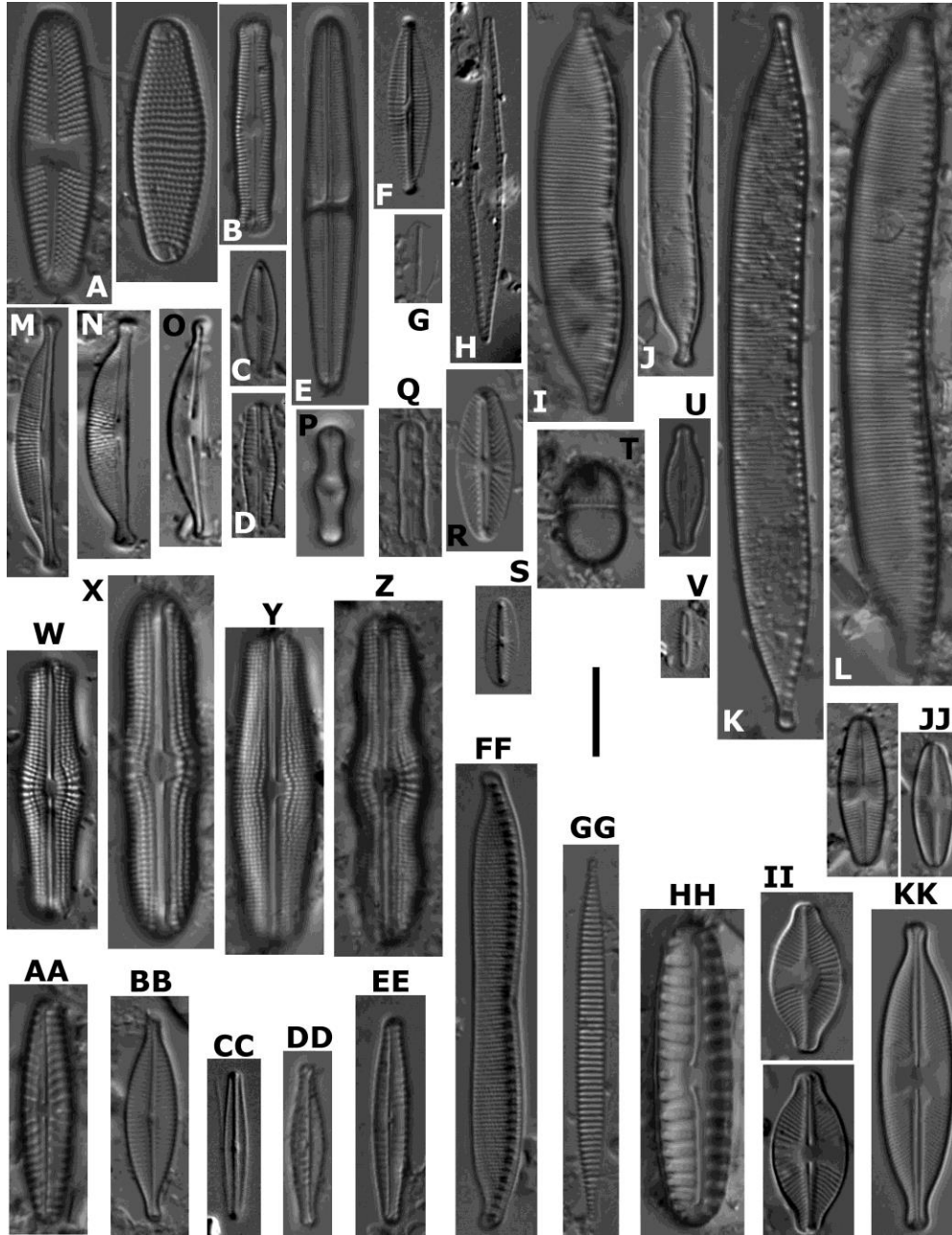


Figure 5: Plate of observed diatoms from the McMurdo Sound Region. The genus *Luticola* is omitted, and is the focus the Appendix. A. *Achananthes taylorensis* raphe and rapheless valve, B. *Chamaepinnularia cymatopleura*, C. *Chamaepinnularia cf. aliena*, D. *Chamaepinnularia* sp. #1, E. *Craspedostauros laevissimus*, F. *Craticula molestiformis*, G. *Fistulifera pelliculosa*, H. *Fragillaria* sp. #1, I. *Hantzschia amphioxys*, J. *Hantzschia amphioxys* f. *muelleri*, K. *Hantzschia cf. abundans/elongata*, L. *Hantzschia hyperaustralis*, M. *Halamphora oligotrophenta* var. #1, N. *Halamphora oligotrophenta* var. #2, O. *Halamphora* ghost valve, P. *Humidophila australis*, Q. *Humidophila arcuata*, R. *Mayamaea atomus*, S. *Mayamaea permitis*, T. *Melosira cf. charcotii*, U. *Microcostatus naumannii*, V. *Microfissurata* sp. #1, W. *Muelleria cryoconicola*, X. *Muelleria meridionalis*, Y. *Muelleria peraustralis*, Z. *Muelleria supra*, AA. *Navicula seibigiana*, BB. *Navicula gregaria*, CC. *Navicula adminii*, DD. *Navicula shackletoni*, EE. *Navicula skuae*(?), FF. *Nitzschia cf. commutata*, GG. *Nitzschia westiorum*, HH. *Pinnularia borealis*, II. *Psammothidium germainii* raphe and rapheless valves, JJ. *Psammothidium papilio* raphe and rapheless valves, KK. *Stauroneis latistauros*. Scale bar is 10µm.

Table 1: New diatom species designations based off work during this dissertation. The genus *Luiccola* is excluded, and in treated in further detail in the Appendix. The corresponding species previously on the Antarctic Diatoms Website database is to the right, along with further comments.

Current taxonomic designations	Exposito et al. 2008 designation	Comments
<i>Achnanthes taylorensis</i> Kelllogg 1980	<i>A. taylorensis</i> Kelllogg 1980	na
<i>Chamaepinnularia cymatopleura</i> (West & West) Cavacini 2006	<i>C. cymatopleura</i> (West & West) Cavacini 2006	likely synonymys <i>Pinnularia detrita</i> , <i>P. quarrenaria</i> , and <i>C. cymatopleura</i> var. 3
<i>Chamaepinnularia</i> sp. 1	na	Resembles <i>C. aliota</i> (Krasske) Van de Vijver & La Côté 2002
<i>Chamaepinnularia</i> sp. 2	na	Only known from a pond on Nustbaum Riegel.
<i>Crocodiscus modestus</i> (Hustedt) Lange-Bertalot 2001	<i>C. modestus</i> (Hustedt) Lange-Bertalot 2000	na
<i>Fistulifera pelliculosa</i> (Kützng) Lange-Bertalot 1997	<i>F. pelliculosa</i> (Kützng) Lange-Bertalot 1997	NOT <i>F. soprophila</i> (Lange-Bertalot & Bonik) Lange-Bertalot 1997
<i>Fragililaria</i> sp. 1	na	Unknown species from Cape Royds.
<i>Hantzschia abundans</i> Lange-Bertalot 1993	<i>H. abundans</i> Lange-Bertalot 1993	Probably a new species. Same as <i>H. elongata</i> in West and West?
<i>Hantzschia amphioxys</i> (Ehrenberg) Grunow 1880	<i>H. amphioxys</i> (Ehrenberg) Grunow 1880	Probably a new species.
<i>Hantzschia amphioxys</i> f. <i>muelleri</i> (Ehrenberg) Ko-Bayashi 1965	<i>H. amphioxys</i> f. <i>muelleri</i> (Ehrenberg) Ko-Bayashi 1965	na
<i>Hantzschia hyperaustrois</i> Van de Vijver & Zidkova 2010	<i>Hantzschia subpraestris</i> Lange-Bertalot 1993	Maybe not <i>H. hyperaustrois</i> , but definitely not <i>H. subpraestris</i> .
<i>Halamphora oligotrophenta</i> (Lange-Bertalot) Levkov 2009	<i>Amphora oligotrophenta</i> (Haworth) Lange-Bertalot & Metzein 1996	na
<i>Halamphora</i> sp. 1	na	One species more narrow, with proximal raphe endings far apart.
<i>Humidophila arcuata</i> (Heiden) Lowe et al. 2014	<i>Diadema contenta</i> (Grunow) Mann 1990	Probably a synonym of <i>Diadema contenta</i> var. <i>porifolia</i> .
<i>Humidophila oustalis</i> (Van de Vijver & Sabbe) Lowe et al. 2014	<i>Diadema persula</i> (Grunow) Mann 1990	na
<i>Mayomaea atomus</i> (Kützng) Lange-Bertalot 1997	<i>M. atomus</i> (Kützng) Lange-Bertalot 1997	Probably a new species. Requires SEM work.
<i>Mayomaea pernis</i> (Hustedt) Buder & Madlin 2008	<i>Mayomaea atomus</i> var. <i>pernis</i> (Hustedt) Lange-Bertalot 1985	Probably a new species. Requires SEM work.
<i>Meiosira charcoii</i> Peragallo 1921	<i>M. charcoii</i> Peragallo 1921	Probably a new species.
<i>Microcostatus noumanni</i> (Hustedt) Lange-Bertalot 1999	<i>Foliola noumanni</i> (Hustedt) Mann 1990	na
<i>Microfissurota</i> sp. 1	na	New species, new genus. Requires SEM work.
<i>Muelleria cryocrotia</i> Stanish & Spaulding 2010	na	na
<i>Muelleria meridionalis</i> Spaulding & Stoermer 1997	<i>M. meridionalis</i> Spaulding & Stoermer 1997	na
<i>Muelleria peroustralis</i> (West & West) Spaulding & Stoermer 1997	<i>M. peroustralis</i> (West & West) Spaulding & Stoermer 1997	na
<i>Muelleria supra Spaulding & Exposito 2008</i>	<i>M. supra Spaulding & Exposito 2008</i>	na
<i>Navicula admirii</i> Roberts & McWinn 1999	<i>Navicula lineola</i> var. <i>peripada</i> Grunow 1894	Still not a <i>Navicula</i> , but <i>N. admirii</i> is a better name than the former
<i>Navicula gregaria</i> Donkin 1861	<i>N. gregaria</i> Donkin 1861	na
<i>Navicula cf. selbigiana</i> Lange-Bertalot 1993	<i>Navicula cincta</i> (Ehrenberg) Raftis 1861	Striae count better fits description of <i>N. selbigiana</i> .
<i>Navicula shackletoni</i> West & West 1911	<i>N. shackletoni</i> West & West 1911	na
<i>Navicula</i> sp. 1	na	Like <i>N. shackletoni</i> , but not <i>N. skucei</i> Alfrinto & Cavacini 2000?
<i>Nitzschia cf. communata</i> Grunow 1880	<i>Hantzschia</i> sp. 5	Soon to be described as a new species of <i>Nitzschia</i> .
<i>Nitzschia westorum</i> (West & West) Van de Vijver 2012	<i>Nitzschia westii</i> (West & West) Kelllogg & Kelllogg 1980	na
<i>Pinnularia borealis</i> Ehrenberg 1843	<i>P. borealis</i> Ehrenberg 1843	Probably a new species of <i>Pinnularia</i> .
<i>Pseudonitzschium papilio</i> (Kelllogg et al.) Van de Vijver & Kopalová 2012	<i>Pseudonitzschium chilidans</i> (John & Hellesman) Lange-Bertalot 1999	na
<i>Pseudonitzschium germainii</i> (Manguin) Sabbe 2003	<i>P. germainii</i> (Manguin) Sabbe 2003	Soon to be described as <i>Pseudonitzschium rostrigermonii</i> .
<i>Stauroneis cf. labstaurus</i> Van de Vijver & Lange-Bertalot 2004	<i>Stauroneis pseudogastrea</i> Lange-Bertalot & Wernum 2004	Probably a new species.

stratigraphy would help shed light onto mat distribution and function. Varin et al. (2010) found evidence of nutrient scavenging in Arctic microbial mats, providing insight to patterns in the observed isotopic signatures in Chapter IV. However, this also raises questions such as: Are mats scavenging nutrients only when needed? How might enzymatic and genetic activity change over an availability gradient? Is there more proteobacteria or heterotrophic organisms in nutrient deficient areas? Do black mats produce more nitrogenase where nitrogen (N) is less available?

Factors contributing to the distribution of mats are not well understood, though efforts have been made to isolate important variables (see one such effort in Figure 7). Four mat types have been observed over the entire length of Taylor Valley, indicating that all types should be available to colonize the entire MDVs. Yet, red mats are rare everywhere, and black mats are far more scarce away from the coast. In the past, this observation has been attributed to the physical environment (ex. Howard-Williams et al. 1989), and it follows that stream gradients become steeper in the Lake Bonney Basin, and streams in general are scarce in the Hoare Basin. These high gradients are unsuitable substrata for black mats, restricting their distribution. Similarly, high sediment streams such as Priscu with mobile substrata are hostile environments for loosely attached mats. However, suitable habitat can only partially explain the distribution of different mat types. For example, Lawson Creek has all mat types at its headwaters despite having a high gradient, and Commonwealth Stream harbors orange, black, and green mats despite having a high sediment load (they are all scoured out by the end of the summer).

Soil nutrient content (specifically N) is thought to limit the dispersal of cryptograms and metazoans in the MDVs (reviewed by Barrett et al. 2006), and by extension it may be reasonable that different mat types may also have elemental constraints. Microbial mat nutrient ratios were



Figure 6: Seal mummy with algae ripe for sampling. Photo courtesy of Steven Crisp.

relatively responsive to nutrient abundance, which may be counter to the notion that mats are able to independently maintain the necessary elemental ratios for metabolism and structure regardless of the external world. Black mat C:N and C:P ratios are inherently high, making it possible that N or P could restrict the distribution of this mat type at low concentrations. Because of the high N:P ratios towards Taylor Glacier, orange mats may outcompete other mat types for P (they had very low C:P and N:P) due to their proximity to the hyporheic zone, which may deprive the water column of nutrients. Black mats are only present in areas with a low N:P ratios, indicating that they could be excluded from these areas because of nutrient competition, and have been previously reported to be more productive in areas with high dissolved P (Howard-Williams et al. 1989), which logically follows given their ability to fix N.

At the landscape-scale, the distribution of mats creates elemental heterogeneity, or "dimensions", with areas of high mat densities being "hotspots", and making the temporal and

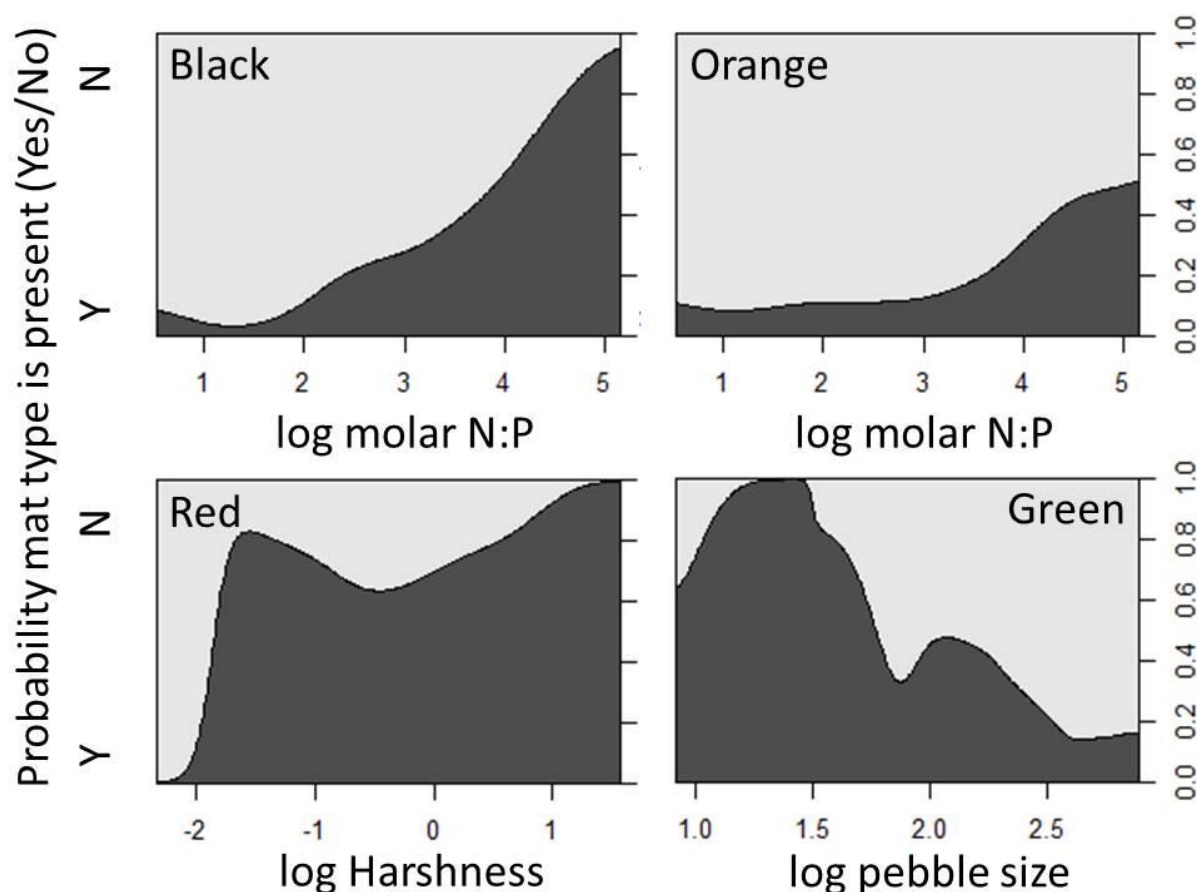


Figure 7: The best predicting variable for determining the presence or absence of a given mat: A) black, B) orange, C) red, and D) green. Data was obtained from 20 years of field notes, as compiled for Chapter III. Variables (gradient, substrata size, dissolved N:P, harshness, and flow variables) were loaded into a glm model, and backwards selection was used to isolate the best explanatory variable for each mat type. Once isolated, logistic regression was used to calculate probabilities shown in the above figures. Note that green mats were also significantly and positively related to gradient, though this result is not pictured.

spatial fluctuation of biomass an important geochemical consideration. Interestingly, changes in biomass of a particular mat community may have effects on the biomass and species diversity of other mat types, as well as the surrounding soil and lake environments. For example, if black mats produce substantial nitrogen which is then used by other mat types where it is limiting (as is suggested in Chapter IV), more biomass may be supported with the presence of black mats than

without. This may be a prime example of facilitation (with black mats being the facilitator), and the MDVs may be an excellent locality to test the Stress Gradient Hypothesis, where facilitation is more likely than competition under high stress environments (Callaway et al. 2002, Maestrel et al. 2009). This may also aid in solving the mystery of what promotes the presence or absence of a mat type in a given year.

Future considerations

While hydrologic and nutrient controls were the main focus of this dissertation, there are other important interactions that will become more influential with time. Radiation is an important consideration for microbial mats (ex. Bonilla et al. 2009), and is probably the reason mat regrowth occurs most aggressively on the undersides of rocks in the early stages (as observed in Chapter II regrowth), until the highly pigmented overstory can be formed. Radiation may also influence temperature, which may be important (Vincent and Howard-Williams 1989, Tang et al. 1997, Howard-Williams and Hawes 2007, Velázquez et al. 2011) given that mats are stimulated under warmer conditions (Howard-Williams et al. 1989, Vincent and Howard-Williams 1989). Increased temperatures may lead to higher biomasses, greater nutrient demand, and potentially altered diatom community structure (Garland 2013). Temperature varies along the longitudinal length of streams (Cozzetto et al. 2006, 2013), being cooler at the headwaters, and equilibrating at intermediate reaches. As most high coverage transects eventually decrease in biomass towards the outlets, it may be worthwhile to investigate interactions with nutrients and temperature to see if coverage may be altered.

Numerous studies have suggested that the strong foehn winds that blow down-valley to the coast (Nylen et al. 2004, Speirs et al. 2010) may be important for the distribution of

organisms and nutrients throughout the MDVs by transporting dried mats (Wharton et al. 1983, Broady 1996, Nkem et al. 2006, Michaud et al. 2012, Šabacká et al. 2012). As carbon and nutrients are often limiting resources for MDV biota in soils and lakes (Barrett et al. 2006), their fluxes may be important for other MDV biological compartments, especially as the nutrient composition of transported material may be far different than the destination (Barrett et al. 2007). Winds may also be important for the exchange of genetic material, and cryoconite holes, which harbor a distinct microbial flora (Wharton et al. 1981, Porazinka et al. 2004, Stanish et al. 2013), may be seeded from winds (Christner et al. 2003). The predicted future increases in foehn events with the Southern Annular Mode (Speirs et al. 2013) may therefore increase ecosystem connectivity throughout the area by redistributing nutrients, carbon, and genes via air.

The transport of mats by flowing waters is also a large component of MDV ecosystem connectivity. Mats are predictably transported to the closed-basin lakes, and have been modeled as a function of discharge and available biomass by Cullis et al. (2014). By analyzing diatom communities in the transported material, there is evidence that biomass may originate far upstream, and drift material has a stoichiometric and isotopic signature similar to that of the parent mat material (Stanish et al., *in preparation*). Streamwater also travels along the shoreline after entering some lakes (Castendyk et al., *in press*), re-allocating material along the “moat” areas where most lake mats reside, and stream organic matter and nutrients has been demonstrated to contribute to lake budgets (Green et al. 1988, Aiken et al. 1996, Foreman et al. 2004, Koch et al. 2010). Collectively, this may suggest that autochthonous material from streams may be important at outlets, adjacent terrestrial habitats, and moat areas, and observations may aid in understanding MDV paleolimnology by interpreting recent material and sediment cores.

RETURN OF THE FLOOD-PULSE

The MDVs are changing. Not only have stream names evolved from “Whangamata” to “Lost Seal” and “Fryxell” to “Canada”, but more concrete, physical observations suggesting change have been made over the last several decades of study. Lake Bonney, rising since Scott’s expedition in 1903 (Bomblies et al. 2001), is now approaching the Priscu Stream algal transect, along with many of the Lake Bonney camp facilities. Few young scientists in the MDVs remember (or realize) that Lake Hoare and Lake Chad were once two separate waterbodies joined in 1992 (McKnight and Andrews 1993). Lake Hoare has since risen sufficiently to alter the flow in Andersen and House Streams, and the shower facility was migrated up-hill during the 2011-12 summer after the lake reached its foundation. On the other side of Canada Glacier, Lake Fryxell has inundated the Aiken Creek and Von Guerard Stream gages, and necessitated new upstream sites for both. Eventually, these rises will result in the relocation of camps such as Fryxell and F6 which sit relatively close to the lake edge, echoing concerns associated with the inundation of the old Lake Vanda camp (Hawes et al. 1999).

Early studies of MDV microbial mat ecology focused on a few streams over a limited number of summers (ex. Vincent and Howard-Williams 1986, Hawes et al. 1992), and the MCMLTER stream monitoring program itself was designed based on the assumption that microbial mats were relatively stable over decadal timescales. Reinforcing this notion was multiple seasons of consistent low flows and a lack of obvious change in the appearance of the mats themselves. However, with the observed disappearance (and appearance) of some mat types in several transects during some very low flow years (1999-00 and 2000-01), their scour during the 2001-02 flood year (Doran et al. 2008, Stanish et al. 2011), and later high flow events in 2008-09 and 2010-11 (ex. Nielsen et al. 2012), reveal that the MDVs are dynamic systems that

exhibit seasonal changes. Recently, the entire streambed mobilized in Huey Creek (2010-11) and Crescent Stream (2011-12), destroying stream gages in place for nearly two decades. Thermokarst has formed in Garwood Valley (Levy et al. 2013) and in Crescent Stream (Fountain et al. 2014), suggesting streambanks themselves are evolving. In addition, previously abandoned or new systems are expected to emerge in higher altitude and up-valley locations (Gooseff et al. 2011) as was the case with Wormherder Creek (Lyons et al. 2005, Nielsen et al. 2012). Collectively, these observations signify a new age for the MCMLTER.

Antarctica is a harsh continent. Because of its isolation and relative inaccessibility, it is the only continent to have never harbored a native human population, and the confirmation of its existence only dates back to the early 1800's. The MDVs were not explored until the 20th century, and were called "valleys of the dead" by Scott's expedition due to the lack of macroscopic life. Regarded as the last pristine continent on Earth, Antarctica is furthermore perceived as a climate change "canary in the coal mine." However, climate patterns here are difficult to interpret by the public as well as scientists due to their counterintuitive nature, and are often highly politicized. The Montreal Protocol, signed to protect the atmosphere by banning ozone depleting CFCs, is generally viewed as a poster child of successful environmental legislation. However, the ozone hole may have kept the Antarctic interior cool over the last few decades (ie. the MDV cooling trend, Doran et al. 2002), and continues to provide proof to many that climate change is a hoax. Thanks to the Protocol's success, Antarctica is ironically projected to warm with its closure (Arblaster and Meehl 2006, Turner et al. 2009, Walsh 2009).

As global resources become scarce, it is likely that the way we view Antarctic legislation in the future may evolve to accommodate geopolitical activity. The Antarctic Treaty is upheld by 49 nations, does not recognize (nor dispute) territorial claims, and leaves residents to the

jurisdiction of their respective governments. Contrary to the notion of a global commons, countries must maintain an active Antarctic research program to remain voting parties in the Treaty. This inequity provides an incentive for poorer governments to build inherently destructive bases with a mission to occupy perceived claims rather than conduct science (let alone minimizing impacts), and completely omits the poorest nations from the international conversation. Furthermore, it is no longer a technological impossibility to plunder Antarctica for its mineral and energy wealth, and without the Madrid Protocol it is possible that widespread exploration would be currently taking place (Tin et al. 2009). The Antarctic Treaty will be revisited in 2048, and subsequent changes will likely outpace new environmental protections, and those created are even less likely to be enforced.

The presence of humans in Antarctica is not an argument for debate. People are here to stay, and as a result, these unique ecosystems will be brought into a new equilibrium state. However, the utility of studying Antarctic streams is non-trivial. In addition to the simplified trophic structure, many resident microbes are endemic (Vyverman et al. 2010), have ancient origins (Bahl et al. 2011, Strunecký et al. 2012), and may have escaped extinction in Antarctica during the last glacial maxima (Vincent et al. 2004, Convey and Stevens 2007). Some evolutionary trajectories have their greatest observed diversity here, such as diatom genera *Luticola* and *Muelleria* (Kopalová et al., *in press*). Furthermore, MDV streams have been used as an astrobiological analogue to study localities otherwise inaccessible through space and time, such as ancient Earth and Mars (Gooseff et al. 2010). While the logistics of sampling the MDVs are physically and politically challenging (ask researcher during the government shutdown), microbial mat research in Antarctica remains our best opportunity to study the limits of Earthly and extraterrestrial life, and is vital to achieving a holistic picture of biology and evolution.

Because of this, it is perhaps our duty to study these unique ecosystems now before they are lost forever.

REFERENCES

- Abram, N.J., Mulvaney, R., Vimeux, F., Phipps, S.J., Turner, J., and England, M.H. 2014. Evolution of the Southern Annular Mode during the past millennium. *Nature Climate Change* 4: 564-569. doi: 10.1038/nclimate2235
- Aiken, G., McKnight, D., Harnish, R., and Wershaw, R. 1996. Geochemistry of aquatic humic substances in the Lake Fryxell Basin, Antarctica. *Biogeochemistry* 34: 157-188.
- Arblaster, J., and Meehl, G. 2006. Contributions of external forcings to Southern Annular Mode trends. *Journal of Climate* 19(12): 2896-2905. doi: 10.1175/JCLI3774.1
- Bahl, J., Lau, M.C.Y., Smith, G.J.D., Vijaykrishna, D., Cary, S.C., Lacap, D.C., Lee, C.K., Papke, R.T., Warren-Rhodes, K.A., Wong, F.K.Y., McKay, C.P., and Pointing, S.B. 2011. Ancient origins determine global biogeography of hot and cold desert cyanobacteria. *Nature Communications* 2: 163. doi: 10.1038/ncomms1167
- Ball, B.A., and Virginia, R.A. 2014. The ecological role of moss in a polar desert: implications for aboveground–belowground and terrestrial–aquatic linkages. *Polar Biology* 37: 651-664. doi: 10.1007/s00300-014-1465-2
- Barrett, J.E., Virginia, R.A., Hopkins, D.W., Aislabie, J., Bargagli, R., Bockheim, J.G., Campbell, I.B., Lyons, W.B., Moorhead, D.L., Nkem, J.N., Sletten, R.S., Steltzer, H., Wall, D.H., and Wallenstein, M.D. 2006. Terrestrial ecosystem processes of Victoria Land, Antarctica. *Soil Biology and Biogeochemistry* 38: 3019-3034. doi: 10.1016/j.soilbio.2006.04.041
- Barrett, J.E., Virginia, R.A., Lyons, W.B., McKnight, D.M., Priscu, J.C., Doran, P.T., Fountain, A.G., Wall, D.H., and Moorhead, D.L. 2007. Biogeochemical stoichiometry of Antarctic dry valley ecosystems. *Journal of Geophysical Research* 112: G01010 doi: 10.1029/2005JG000141
- Bomblies, A., McKnight, D.M., and Andrews, E.D. 2001. Retrospective simulation of lake-level rise in Lake Bonney Based on recent 21-yr record: indication of recent climate change in the McMurdo Dry Valleys, Antarctica. *Journal of Paleolimnology* 25: 477-492.
- Bonilla, S., Rautio, M., and Vincent, W.F. 2009. Phytoplankton and phytobenthos pigment strategies: implications for algal survival in the changing Arctic. *Polar Biology* 32(9): 1293-1303. doi: 10.1007/s00300-009-0626-1

- Broady, P.A. 1996. Diversity, distribution and dispersal of Antarctic terrestrial algae. *Biodiversity and Conservation* 5: 1307-1335.
- Broady, P.A., and Kibblewhite, A.L. 1991. Morphological characterization of the Oscillatoriales (Cyanobacteria) from Ross Island and Southern Victoria Land, Antarctica. *Antarctic Science* 3(1): 35-45.
- Burkins, M.B., Virginia, R.A., Chamberlain, C.P., and Wall, D.H. 2000. Origin and distribution of soil organic matter in Taylor Valley, Antarctica. *Ecology* 81(9): 2377-2391.
- Callaway, R.M., Brooker, R.W., Choler, P., Kikvidze, Z., Lortie, C.J., Michalet, F., Paolini, L., Pugnaire, F.I., Newingham, B., Aschehoug, E.T., Armas, C., Kikodze, D., and Cook, B.J. 2002. Positive interactions among alpine plants increase with stress. *Nature* 417: 844-848. doi: 10.1038/nature00812
- Castendyk, D. *In press*. Pressure-driven, shoreline currents in a perennially ice-covered, pro-glacial lake in Antarctica, identified from a LiCl tracer injected into a pro-glacial stream. doi: 10.1002/hyp.10352
- Chown, S.L., Lee, J.E., Hughes, K.A., Barnes, J., Barret, P.J., Bergstrom, D.M., Convey, P., Cowan, D.A., Crosbie, K., Dyer, G., Frenot, Y., Grant, S.M., Herr, D., Kennicutt II, M.C., Lamers, M., Murray, A., Possingham, H.P., Reid, K., Riddle, M.J., Ryan, P.G., Sanson, L., Shaw, J.D., Sparrow, M.D., Summerhayes, C., Terauds, A., and Wall, D.H. 2012. Challenges to future conservation of the Antarctic. *Science* 337(6091): 158-159. doi: 10.1126/science.1222821
- Christner, B.C., Kvitko, B.H., and Reeve, J.N. 2003. Molecular Identification of Bacteria and Eukarya Inhabiting an Antarctic Cryoconite Hole. *Extremophiles* 7: 177-183.
- Convey, P., and Stevens, M.I. 2007. Antarctic biodiversity. *Science* 317: 1877-1878.
- Cozzetto, K.D., Bencala, K.E., Gooseff, M.N., and McKnight, D.M. 2013. The influence of stream thermal regimes and preferential flow paths on hyporheic exchange in a glacial meltwater stream. *Water Resources Research* 49: 1-18.
- Cozzetto, K., McKnight, D., Nylen, T., and Fountain, A. 2006. Experimental investigations into processes controlling stream and hyporheic temperatures, Fryxell Basin, Antarctica. *Advances in Water Resources* 29: 130-153.
- Cullis, J.D.S., Stanish, L.F., and McKnight, D.M. 2014. Diel flow pulses drive particulate organic matter transport from microbial mats in a glacial meltwater stream in the McMurdo Dry Valleys. *Water Resources Research* 50. doi: 10.1002/2013WR014061.
- Dodds, W.K., Collins, S.M., Hamilton, S.K., Tank, J.L., Johnson, S., Webster, J.R., Simon, K.S., Whiles, M.R., Rantala, H.M., McDowell, W.H., Peterson, S.D., Riis, T., Crenshaw, C.L., Thomas, S.A., Kristensen, P.B., Cheever, B.M., Flecker, A.S., Griffiths, N.A., Crowl, T.,

- Rosi-Marshall, E.J., El-Sabaawi, R., and Martí, E. 2014. You are not always what we think you eat: selective assimilation across multiple whole-stream isotopic tracer studies. *Ecology* 95(10): 2757-2767.
- Doran, P.T., McKay, C.P., Fountain, A.G., Nylen, T., McKnight, D.M., Jaros, C., and Barrett, J.E. 2008. Hydrologic response to extreme warm and cold summers in the McMurdo Dry Valleys, East Antarctica. *Antarctic Science* 20: 499-509. doi: 10.1017/S0954102008001272
- Foreman, C.M., Wolf, C.F., and Priscu, J.C. 2004. Impact of episodic warming events on the physical, chemical, and biological relationships of lakes in the McMurdo Dry Valleys, Antarctica. *Aquatic Geochemistry* 10: 239-268.
- Fountain, A.G., Levy, J.S., Gooseff, M.N., and Van Horn, D. 2014. The McMurdo Dry Valleys: a landscape on the threshold of change. *Geomorphology* 225: 25-35. doi: 10.1016/j.geomorph.2014.03.044
- Fritsch, F.E. 1912. Freshwater algae. National Antarctic “Discovery” Expedition 1901-1904. *British Museum of Natural History* 6: 1-66.
- Garland, D.D. 2013. Influences of temperature on antarctic freshwater diatom growth rates in culture. Master’s Thesis, University of Colorado.
- Gooseff, M.N., McKnight, D.M., Carr, M.H., and Baeseman, J. 2010. Antarctic McMurdo Dry Valley stream ecosystems as an analog to fluvial systems on Mars. In Doran, P.T., Lyons, W.B., and McKnight, W.B., Eds. *Life in Antarctic deserts and other cold dry environments*. Cambridge, UK: Cambridge University Press, 139-159.
- Gooseff, M.N., McKnight, D.M., Doran, P., Fountain, A.G., and Lyons, W.B. 2011. Hydrological connectivity of the landscape of the McMurdo Dry Valleys, Antarctica. *Geography Compass* 5/9: 666–681. doi: 10.1111/j.1749-8198.2011.00445.x
- Green, W.J., Angle, M.P., and Chave, K.E. 1988. The geochemistry of Antarctic streams and their role in the evolution of four lakes in the McMurdo Dry Valleys. *Geochimica et Cosmochimica Acta* 52: 1265-1274.
- Hawes, I., Smith, R., and Sutherland, D. 1999. Development of microbial mats on contaminated soils from the former site of Vanda Station, Antarctica. *New Zealand Natural Sciences* 24: 53-68.
- Howard-Williams, C., Priscu, J.C., and Vincent, W.F. 1989. Nitrogen dynamics in two Antarctic streams. *Hydrobiologia* 172: 51-61.
- Huiskes, A.H.L., Gremmen, N.J.M., Bergstrom, D.M., Frenot, Y., Hughes, K.A., Imura, S., Kiefer, K., Lebouvier, M., Lee, J.E., Tsujimoto, M., Ware, C., Van de Vijver, B., and Chown, S.L. 2014. Aliens in Antarctica: Assessing transfer of plant propagules by human visitors to reduce invasion risk. *Biological Conservation* 171: 278-284.

- Humphries, P., Keckeis, H., and Finlayson, B. 2014. The River Wave Concept: Integrating river ecosystem models. *BioScience* 64: 870-882. doi: 10.1093/biosci/biu130
- Izaguirre, I., and Pizarro, H. 1998. Epilithic algae in a glacial stream at Hope Bay (Antarctica). *Polar Biology* 19: 24-31.
- John, D.M. 2003. Filamentous and plantlike green algae. In Wehr, J.D., and Sheath, R.G., Eds. *Freshwater algae of North America: Ecology and classification*. San Diego, CA: Academic Press, 311-352.
- John, D.M., Whitton, B.A., and Brook, A.J. 2002. *The Freshwater Algal Flora of the British Isles: An identification guide to freshwater and terrestrial algae*. Cambridge, UK: Cambridge University Press and The Natural History Museum, 702.
- Junk, W.J., Bayley, P.B., and Sparks, R.E. 1989. The flood pulse concept in river-floodplain systems. *Canadian Special Publication of Fisheries and Aquatic Sciences* 106: 110-127.
- Koch, J.C., McKnight, D.M., and Baeseman, J.L. 2010. Effect of unsteady flow on nitrate loss in an oligotrophic, glacial meltwater stream. *Journal of Geophysical Research-Biogeosciences* 115: G01001.
- Komárek, J. 2007. Phenotype diversity of the cyanobacterial genus *Leptolyngbya* in the Maritime Antarctic. *Polish Polar Research* 28(3): 211-231.
- Komárek, J., and Anagnostidis, K. 2005. Cyanoprokaryota - 2. Teil: Oscillatoriales. In Buedel, B., Krienitz, L., Gaertner, G. and Schagerl, M., Eds. *Süßwasserflora von Mitteleuropa*, Band 19/2. Heidelberg: Elsevier/Spektrum, 759.
- Komárek, J., J. Kaštovsky, S. Ventura, S. Turicchia, and J. Šmarda. 2009. The cyanobacterial genus *Phormidesmis*. *Algological Studies* 129: 41-59. doi: 10.1127/1864-1318/2009/0129-0041
- Kopalová, K., Kociolek, J.P., Lowe, R.L., Zidarova, R., and Van De Vijver, B. *In press*. Five new species of the genus *Humidophila* (Bacillariophyta) from the Maritime Antarctic Region. *Diatom Research*. doi: 10.1080/0269249X.2014.998714
- Kopalová, K., Nedbalová, L., Nyvlt, D., Elster, J., and Van de Vijver, B. 2013. Diversity, ecology and biogeography of the freshwater diatom communities from Ulu Peninsula (James Ross Island, NE Antarctic Peninsula). *Polar Biology* 36(7): 933-948. doi: 10.1007/s00300-013-1317-5
- Kopalová, K., Ochýra, R., Nedbalová, L., and Van de Vijver, B. 2014. Moss-inhabiting diatoms from two contrasting Maritime Antarctic islands. *Plant Ecology and Evolution* 147(1): 67-84.

- Kopalová, K., and Van de Vijver, B. 2013. Structure and ecology of freshwater benthic diatom communities from Byers Peninsula, Livingston Island, South Shetland Island. *Antarctic Science* 25(2): 239-253. doi: 10.1017/S0954102012000764
- Kováčik, L., and Pereira, A.B. 2001. Green alga *Prasiola crispa* and its lichenized form *Mastodia tessellata* in Antarctic environment: General aspects. *Nova Hedwigia* 123: 465-478.
- Levy, J.S., Fountain, A.G., Dickson, J.L., Head, J.W., Okal, M., Marchant, D.R., and Watters, J. 2013. Accelerated thermokarst formation in the McMurdo Dry Valleys, Antarctica. *Scientific Reports* 3: 2269. doi: 10.1038/srep02269
- Lyons, W.B., Welch, K.A., Carey, A.E., Doran, P.T., Wall, D.H., Virginia, R.A., Fountain, A.G., Csathó, B.M., and Tremper, C.M. 2005. Groundwater seeps in Taylor Valley, Antarctica: an example of a subsurface melt event. *Annals of Glaciology* 40: 200-206. doi: 10.3189/172756405781813609
- Maestrel, F.T., Callaway, R.M., Valladares, F., and Lortie, C.J. 2009. Refining the stress-gradient hypothesis for competition and facilitation in plant communities. *Journal of Ecology* 97(2): 199-205. doi: 10.1111/j.1365-2745.2008.01476.x
- McKnight, D.M., and Andrews, E.D. 1993. Potential hydrologic and geochemical consequences of the 1992 merging of Lake Chad with Lake Hoare in Taylor Vally. *Antarctic Journal* 249-251.
- Michaud, A.B., Šabacká, M. and Priscu, J.C. 2012. Cyanobacterial diversity across landscape units in a polar desert: Taylor Valley, Antarctica. *FEMS Microbiology Ecology* 82(2): 268-278. doi: 10.1111/j.1574-6941.2012.01297.x
- Moniz, M.B.J., Rindi, F., Novis, P.M., Broady, P.A., and Guiry, M.D. 2012. Molecular phylogeny of Antarctic *Prasiola* (Prasiolales, Trebouxiophyceae) reveals extensive cryptic diversity. *Journal of Phycology* 48: 940-955. doi: 10.1111/j.1529-8817.2012.01172.x
- Nielsen, U.N., Wall, D.H., Adams, B.J., Virginia, R.A., Ball, B.A., Gooseff, M.N., and McKnight, D.M. 2012. The ecology of pulse events: insights from an extreme climatic event in a polar desert ecosystem. *Ecosphere* 3(2): 17. doi: 10.1890/ES11-00325.1
- Nkem, J.N., Wall, D.H., Virginia, R.A., Barrett, J.E., Broos, E.J., Porazinska, D.L., and Adams, B.J. 2006. Wind Dispersal of Soil Invertebrates in the Mcmurdo Dry Valleys, Antarctica. *Polar Biology* 29: 346-352.
- Nylen, T.H., Fountain, A.G., and Doran, P.T. 2004. Climatology of katabatic winds in the McMurdo Dry Valleys, southern Victoria Land, Antarctica. *Journal of Geophysical Research-Atmospheres* 109(D3): D03114.

- Ohtani, S., Suvama, K., and Kanda, H. 2000. Environmental monitoring by means of soil algae and microorganisms in the vicinity of Syowa Station. *Nankyoku Shiryo (Antarctic Record)* 44: 265-276.
- Paerl, H.W., Pinckney, J.L., and Steppe, T.F. 2000. Cyanobacterial-bacterial mat consortia: examining the functional unit of microbial survival and growth in extreme environments. *Environmental Microbiology* 2(1): 11-26.
- Porazinska, D.L., Fountain, A.G., Nylen, T.H., Tranter, M., Virginia, R.A., and Wall, D.H. 2004. The Biodiversity and Biogeochemistry of Cryoconite Holes from McMurdo Dry Valley Glaciers, Antarctica. *Arctic Antarctic and Alpine Research* 36: 84-91.
- Richard, Y., Rouault, M., Pohl, B., Cr  tat, J., Duclot, I., Taboulot, S., Reason, C.J.C., Macron, C., and Buiron, D. 2013. Temperature changes in the mid- and high- latitudes of the Southern Hemisphere. *International Journal of Climatology* 33: 1948-1963.
-   aback  , M., Priscu, J.C., Basagic, H.J., Fountain, A.G., Wall, D.H., Virginia, R.A., and Greenwood, M.C. 2012. Aeolian flux of biotic and abiotic material in Taylor Valley, Antarctica. *Geomorphology* 155-156: 102-111. doi: 10.1016/j.geomorph.2011.12.009
- Sakaeva, A. 2014. Ecology and biogeography of freshwater diatoms in ponds of McMurdo Dry Valleys and parts of the Ross Island. Master's Thesis, University of Colorado.
- Seaburg, K.G., Parker, B.C., Prescott, G.W., and Whitford, L.A. 1979. The algae of southern Victoria Land. *Bibliotheca Phycologia* 46: 169.
- Souffreau, C., Vanormelingen, P., Van de Vijver, B., Isheva, T., Verleyen, E., Sabbe, K., and Vyverman, W. 2013. Molecular Evidence for Distinct Antarctic Lineages in the Cosmopolitan Terrestrial Diatoms *Pinnularia borealis* and *Hantzschia amphioxys*. *Protist* 164(1): 101-115. doi: 10.1016/j.protis.2012.04.001
- Speirs, J.C., Steinhoff, D.F., McGowan, H.A., Bromwich, D.H., and Monaghan, A.J. 2010. Foehn Winds in the McMurdo Dry Valleys, Antarctica: The Origin of Extreme Warming Events. *Journal of Climate* 23: 3577-3598. doi: 10.1175/2010JCLI3382.1
- Speirs, J.C., McGowan, H.A., Steinhoff, D.F., and Bromwich, D.H. 2013. Regional climate variability driven by foehn winds in the McMurdo Dry Valleys, Antarctica. *International Journal of Climatology* 33: 945-958. doi: 10.1002/joc.3481
- Stanish, L.F., Bagshaw, E.A., McKnight, D.M., Fountain, A.G., and Tranter, M. 2013. Environmental factors influencing diatom communities in Antarctic cryoconite holes. *Environmental Research Letters* 8: 045006. doi: 10.1088/1748-9326/8/4/045006
- Stanish, L.F., O'Neill, S.P., Gonzalez, A., Legg, T.M., Knelman, J., McKnight, D.M., Spaulding, S.A., and Nemergut, D.R. 2012. Bacteria and diatom co-occurrence patterns in microbial

- mats from polar desert streams. *Environmental Microbiology* 15(4): 1115-1131. doi: 10.1111/j.1462-2920.2012.02872.x
- Stanish, L.F., and Spear, J.R. 2013. Diatom ecology and microbial mat structure and function in Antarctic Dry Valleys. *Palaios* 28(5): 267-269. doi: 10.2110/palo.2013.S03
- Stanley, E.H., Fisher, S.G., and Jones Jr, J.B. 2004. Effects of water loss on primary production: A landscape-scale model. *Aquatic Sciences* 66: 130-138. doi: 10.1007/s00027-003-0646-9
- Strunecký, O., Elster, J., and Komárek, J. 2012. Molecular clock evidence for survival of Antarctic cyanobacterial (*Oscillatoriales*, *Phormidium autumnale*) from Paleozoic times. *FEMS Microbiology Ecology* 82: 482-490. doi: 10.1111/j.1574-6941.2012.01426.x
- Strunecký, O., Komárek, J., Johansen, J., Lukešová, A., and Elster, J. 2013. Molecular and morphological criteria for revision of the genus *Microcoleus* (Oscillatoriales, cyanobacteria). *Journal of Phycology* 49: 1167-1180. doi: 10.1111/jpy.12128
- Tang, E.P.Y., Tremblay, R., and Vincent, W.F. 1997. Cyanobacterial dominance of polar freshwater ecosystems: are high-latitude mat-formers adapted to low temperature? *Journal of Phycology* 33: 171-181.
- Taton, A., Grubisic, S., Balthasart, P., Hodgson, D.A., Laybourn-Parry, J., and Wilmotte, A. 2006. Biogeographical distribution and ecological ranges of benthic cyanobacteria in East Antarctic lakes. *FEMS Microbiology Ecology* 57: 272-289. doi: 10.1111/j.1574-6941.2006.00110.x
- Taton, A., Grubisic, S., Brambilla, E., De Wit, R., and Wilmotte, A. 2003. Cyanobacterial diversity in natural and artificial microbial mats of Lake Fryxell (McMurdo Dry Valleys, Antarctica): a morphological and molecular approach. *Applied and Environmental Microbiology* 69(9): 5157-5169. doi: 10.1128/AEM.69.9.5157-5169.2003
- Tin, T., Fleming, Z.L., Hughes, K.A., Ainley, D.G., Convey, P., Moreno, C.A., Pfeiffer, S., Scott, J., and Snapes, I. 2009. Impacts of local human activities on the Antarctic environment. *Antarctic Science* 21(1): 3-33. doi: 10.1017/S0954102009001722
- Tockner, K., Malard, F., and Ward, J.V. 2000. An extension of the flood pulse concept. *Hydrological Processes* 14: 2861-2883.
- Turner, J., Arthern, R., Bromwich, D., Marshall, G., Worby, T., Bockheim, J., Di Prisco, G., Verde, C., Convey, P., Roscoe, H., Jones, A., Vaughan, D., Woodworth, P., Scambos, T., Cook, A., Lenton, A., Comiso, J., Gugliemin, M., Summerhayes, C., Meredith, M., Naveira-Garabato, A., Chown, S., Stevens, M., Adams, B., Worland, R., Hennion, F., Huiskes, A., Bergstrom, D., Hodgson, D.A., Bindenschadler, R., Bargagli, R., Metzl, N., Van Der Veen, K., Monaghan, A., Speer, K., Rintoul, S., Hellmer, H., Jacobs, S., Heywood, K., Holland, D., Yamanouchi, T., Barbante, C., Bertler, N., Boutron, C., Hong, S., Mayewski, P., Fastook, J., Newsham, K., Robinson, S., Forcarda, J., Trathan, P., Smetacek, V., Gutt, J., Pörtner, H.-O.,

- Peck, L., Gili, J.-M., Wiencke, C., Fahrback, E., Atkinson, A., Webb, D., Isla, E., Orejas, C., Rossi, S. and Shanklin, J. 2009. The instrumental period. In Turner, J., Bindschadler, R., Convey, P., Di Prisco, G., Fahrback, E., Gutt, J., Hodgson, D.A., Mayewski, P.A. and Summerhayes, C.P., Eds. *Antarctic climate change and the environment*. Cambridge, UK: Scientific Committee for Antarctic Research, 183–298.
- Vannote, R.L., Minshall, G.W., Cummins, K.W., Sedell, J.R., and Cushing, C.E. 1980. The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* 37: 130-137.
- Varin, T., Lovejoy, C., Jungblut, A.D., Vincent, W.F., and Corbeil, J. 2010. Metagenomic profiling of Arctic microbial mat communities as nutrient scavenging and recycling systems. *Limnology and Oceanography* 55: 1901-1911. doi:10.4319/lo.2010.55.5.1901
- Velázquez, D., Rochera, C., Camacho, A., and Quesada, A. 2011. Temperature effects on carbon and nitrogen metabolism in some Maritime Antarctica freshwater phototrophic communities. *Polar Biology* 34: 1045-1055.
- Vincent, W.F., and Howard-Williams, C. 1989. Microbial communities in southern Victoria Land streams (Antarctica) II. The effects of low temperature. *Hydrobiologia* 172: 39-49.
- Vincent, W.F., and James, M.R. 1996. Biodiversity in extreme aquatic environments: Lakes, ponds, and streams of the Ross Sea sector, Antarctica. *Biodiversity and Conservation* 5: 1451-1471.
- Vincent, W.F., Mueller, D.R., and Bonilla S. 2004. Ecosystems on ice: the microbial ecology of Markham Ice Shelf in the high Arctic. *Cryobiology* 48: 103–112.
- Vyverman, W., Verleyen, E., Sabbe, K., Vanhoutte, K., Sterken, M., Hodgson, D.A., Mann, D.G., Juggins, S., Van de Vijver, B., Jones, V., Flower, R., Roberts, D., Chepurnov, V.A., Kilroy, C., Vanormelingen, P., and de Wever, A. 2007. Historical processes constrain patterns in global diatom diversity. *Ecology* 88(8): 1924–1931.
- Vyverman, W., Verleyen, E., Wilmotte, A., Hodgson, D., Willems, A., Peeters, K., Van de Vijver, B., De Wever, A., Leliaert, F., and Sabbe, K. 2010. Evidence for widespread endemism among Antarctic micro-organisms. *Polar Science* 4: 103-113. doi: 10.1016/j.polar.2010.03.006
- Walsh, J.E. 2009. A comparison of Arctic and Antarctic climate change, present and future. *Antarctic Science* 21(3): 179-188. doi: 10.1017/S0954102009001874.
- Ward, J.V., and Stanford, J.A. 1983. The intermediate disturbance hypothesis: an explanation for biotic diversity patterns in lotic ecosystems. In Fontaine, T.D. and Bartell, S.M., Eds. *Dynamics of lotic ecosystems*. Ann Arbor, MI, Ann Arbor Science Publishers, 347-356.
- Ward J.V., and Stanford, J.A. 1995. The serial discontinuity concept: Extending the model to floodplain rivers. *Regulated Rivers: Research & Management* 10(2-4): 159-168. doi:

- West, G.S. 1927. A treatise on the British freshwater algae: in which are included all the pigmented Protophyta hitherto found in British freshwaters. Cambridge, UK: The University Press, 534 pp.
- West, W. and West, G.S. 1911. Freshwater algae. British Antarctic Expedition (1907–1909) Science Report. Biology 1: 263–298.
- Wharton Jr., R.A., Lyons, W.B., and Des Marais, D.J. 1993. Stable isotopic biogeochemistry of carbon and nitrogen in a perennially ice-covered Antarctic lake. *Chemical Geology* 107: 159–172. doi: 10.1016/0009-2541(93)90108-U
- Wharton Jr, R.A., Parker B.C., and Simmons Jr, G.M. 1983. Distribution, species composition and morphology of algal mats in Antarctic dry valley lakes. *Phycologia* 22(4): 355–365.
- Wharton, R.A., Vinyard, W.C., Parker, B.C., Simmons, G.M., Seaburg, K.G. 1981. Algae in cryoconite holes on Canada Glacier in southern Victoria Land, Antarctica. *Phycologia* 20: 208–211.
- Wyatt, K.H., Rober, A.R., Schmidt, N., and Davison, I.R. 2014. Effects of desiccation and rewetting on the release and decomposition of dissolved organic carbon from benthic macroalgae. *Freshwater Biology* 59: 407–416.
- Zeglin, L.H., Dahm, C.N., Barrett, J.E., Gooseff, M.N., Fitzpatrick, S.K., and Takacs-Vesbach, C.D. 2011. Bacterial community structure along moisture gradients in the parafluvial sediments of two ephemeral desert streams. *Microbial Ecology* 61: 1–14.

BIBLIOGRAPHY

- Abe, S.I., Sakano, H., Kobayashi, S., and Kitano, S. 2014. Stable carbon isotope variability associated with taxonomic composition of lotic benthic algae. *Phycological Research* 62(1): 73-76.
- Abram, N. J., Mulvaney, R., Vimeux, F., Phipps, S.J., Turner, J., and England, M.H. 2014. Evolution of the Southern Annular Mode during the past millennium. *Nature Climate Change* 4: 564–569. doi:10.1038/nclimate2235
- Aiken, G., McKnight, D., Harnish, R., and Wershaw, R. 1996. Geochemistry of aquatic humic substances in the Lake Fryxell Basin, Antarctica. *Biogeochemistry* 34: 157-188.
- Alger, A.S., McKnight D.M., Spaulding S.A., Tate, C.M., Shupe, G.H., Welch, K.A., Edwards, R., Andrews, E.D., and House, H.R. 1997. Ecological processes in a cold desert ecosystem: the abundance and species distribution of algal mats in glacial meltwater streams in Taylor Valley, Antarctica. Institute of Arctic and Alpine Research Occasional Paper 51.
- Andersen, D.T., Sumner, D.Y., Hawes, I., Webster-Brown, J., and McKay, C.P.. 2011. Discovery of large conical stromatolites in Lake Untersee, Antarctica. *Geobiology* 9:280-293. doi: 10.1111/j.1472-4669.2011.00279.x
- Arblaster, J., and Meehl, G. 2006. Contributions of external forcings to Southern Annular Mode trends. *Journal of Climate* 19: 2896-2905.
- Ayres, E., Nkem, J.N., Wall, D.H., Adams, B.J., Barrett, J.E., Broos, E.J., Parsons, A.N., Powers, L.E., Simmons, B.L., and Virginia, R.A. 2008. Effects on human trampling on populations of soil fauna in the McMurdo Dry Valleys, Antarctica. *Conservation Biology* 22: 1544-1551.
- Badger, M.R., Hanson, D., and Price, G.D. 2002. Evolution and diversity of CO₂ concentrating mechanisms in cyanobacteria. *Functional Plant Biology* 29(3): 161-173.
- Bahl, J., Lau, M.C.Y., Smith, G.J.D., Vijaykrishna, D., Cary, S.C., Lacap, D.C., Lee, C.K., Papke, R.T., Warren-Rhodes, K.A., Wong, F.K.Y., McKay, C.P., and Pointing, S.B. 2011. Ancient origins determine global biogeography of hot and cold desert cyanobacteria. *Nature Communications* 2: 163. doi: 10.1038/ncomms1167
- Ball, B.A., and R.A. Virginia. 2014. The ecological role of moss in a polar desert: implications for aboveground–belowground and terrestrial–aquatic linkages. *Polar Biology* 37: 651–664. doi: 10.1007/s00300-014-1465-2
- Barrett, J.E., Virginia, R.A., Hopkins, D.W., Aislabie, J., Bargagli, R., Bockheim, J.G, Campbell, I.B., Lyons, W.B., Moorhead, D.L., Nkem, J.N., Sletten, R.S., Steltzer, H., Wall, D.H., and Wallenstein, M.D. 2006. Terrestrial ecosystem processes of Victoria Land, Antarctica. *Soil Biology and Biogeochemistry* 38: 3019-3034. doi: 10.1016/j.soilbio.2006.04.041

- Barrett, J.E., Virginia, R.A., Lyons, W.B., McKnight, D.M., Priscu, J.C., Doran, P.T., Fountain, A.G., Wall, D.H., and Moorhead, D.L. 2007. Biogeochemical stoichiometry of Antarctic Dry Valley ecosystems. *Journal of Geophysical Research* 112: G01010. doi: 10.1029/2005JG000141
- Barrett, J.E., Virginia, R.A., Wall, D.H., Doran, P.T., Fountain, A.G., Welch, K.A., and Lyons, W.B. 2008. Persistent effects of a discrete warming event on a polar desert ecosystem. *Global Change Biology* 14: 1-13.
- Bate, D.B., Barrett, J.E., Poage, M.A., and Virginia, R.A. 2008. Soil phosphorus cycling in an Antarctic polar desert. *Geoderma* 144(1): 21-31. doi:10.1016/j.geoderma.2007.10.007
- Bates, D., Maechler, M., Bolker, B. and Walker, S. 2014. lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-7. Available: <http://CRAN.R-project.org/package=lme4>
- Biggs, B.J.F., Goring, D.G., and Nikora V.I. 1998. Subsidy and stress responses of stream periphyton to gradients in water velocity as a function of community growth form. *Journal of Phycology* 34: 598-607.
- Biggs, B.J.F., and Thomsen, H.A. 1995. Disturbance in stream periphyton by perturbations in shear stress: Time to structural failure and differences in community resistance. *Journal of Phycology* 31: 233-241.
- Bishop, J.L., Lougear, A., Newton, J., Doran, P.T., Froeschl, H., Trautwein, A.X., Korner, W. and Koeberl, C. 2001. Mineralogical and geochemical analyses of Antarctic lake sediments: A study of reflectance and Mössbauer spectroscopy and C, N, and S isotopes with applications for remote sensing on Mars. *Geochimica et Cosmochimica Acta* 65: 2875–2897.
- Bixby, R.J., Benstead, J.P., Douglas, M.M., and Pringle, C.M. 2009. Relationships of stream algae community structure to catchment deforestation in eastern Madagascar. *Journal of the North American Benthological Society* 28: 466-479.
- Bombles, A., McKnight, D.M., and Andrews, E.D. 2001. Retrospective simulation of lake-level rise in Lake Bonney Based on recent 21-yr record: indication of recent climate change in the McMurdo Dry Valleys, Antarctica. *Journal of Paleolimnology* 25: 477-492.
- Bonilla, S., Rautio, M., and Vincent, W.F. 2009. Phytoplankton and phytobenthos pigment strategies: implications for algal survival in the changing Arctic. *Polar Biology* 32: 1293-1303. doi: 10.1007/s00300-009-0626-1
- Bonilla, S., Villeneuve, V., and Vincent, W.F. 2005. Benthic and planktonic algal communities in a high arctic lake: pigment structure and contrasting responses to nutrient enrichment. *Journal of Phycology* 41: 1120-1130. doi: 10.1111/j.1529-8817.2005.00154.x

- Brabandere, L.D., Frazer, T.K. and Montoya, J.P. 2007. Stable nitrogen isotope ratios of macrophytes and associated periphyton along a nitrate gradient in two subtropical, spring-fed streams. *Freshwater Biology* 52: 1564–1575. doi: 10.1111/j.1365-2427.2007.01788.x
- Broady, P.A. 1996. Diversity, distribution and dispersal of Antarctic terrestrial algae. *Biodiversity and Conservation* 5: 1307-1335.
- Broady, P.A., and Kibblewhite, A.L. 1991. Morphological characterization of the Oscillatoriales (Cyanobacteria) from Ross Island and Southern Victoria Land, Antarctica. *Antarctic Science* 3(1): 35-45.
- Burkins, M.B., Virginia, R.A., Chamberlain, C.P., and Wall, D.H. 2000. Origin and distribution of soil organic matter in Taylor Valley, Antarctica. *Ecology* 81(9): 2377-2391. doi: 10.1890/0012-9658(2000)081[2377:OADOSO]2.0.CO;2
- Burnham, K.P., and Anderson, D.R. 2002. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. New York: Springer New York, 488.
- Callaway, R.M., Brooker, R.W., Choler, P., Kikvidze, Z., Lortie, C.J., Michalet, F., Paolini, L., Pugnaire, F.I., Newingham, B., Aschehoug, E.T., Armas, C., Kikodze, D., and Cook, B.J. 2002. Positive interactions among alpine plants increase with stress. *Nature* 417: 844-848. doi: 10.1038/nature00812
- Campbell, I.B., Claridge, G.G.C. and Balks, M.R. 1998. Short and long-term impacts of human disturbance on snow-free surfaces in Antarctica. *Polar Record* 34: 15-24.
- Cardinale, B.J., Palmer, M.A., Swan, C.M., Brooks, S., and Poff, N.L. 2002. The influence of substrate heterogeneity on biofilm metabolism in a stream ecosystem. *Ecology* 83: 412–422.
- Castendyk, D. *In press*. Pressure-driven, shoreline currents in a perennially ice-covered, proglacial lake in Antarctica, identified from a LiCl tracer injected into a pro-glacial stream. doi: 10.1002/hyp.10352
- Chapman, W.L., and Walsh, J.E. 2007. A synthesis of Antarctic temperatures. *Journal of Climate* 20: 4096-4117.
- Chinn, T.J. 1993. Physical hydrology of the Dry Valley lakes. In Green, W.J. and Friedmann, E.I., Eds. *Physical and Biogeochemical Processes in Antarctic Lakes*. Antarctic Research Series, Washington, D.C.: American Geophysical Union, 1-52.
- Chown, S.L., Huiskes, A.H.L., Gremmen, N.J.M., Lee, J.E., Terauds, A., Crosbie, K., Frenot, Y., Hughes, K.A., Imura, S., Kiefer, K., Lebouvier, M., Raymond, B., Tsujimoto, M., Ware, C., Van de Vijver, B., and Bergstrom, D.M. 2012. Continent-wide risk assessment for the establishment of nonindigenous species in Antarctica. *Proceedings of the National Academy of Science* 109(13): 4938-4943.

- Chown, S.L., Lee, J.E., Hughes, K.A., Barnes, J., Barret, P.J., Bergstrom, D.M., Convey, P., Cowan, D.A., Crosbie, K., Dyer, G., Frenot, Y., Grant, S.M., Herr, D., Kennicutt II, M.C., Lamers, M., Murray, A., Possingham, H.P., Reid, K., Riddle, M.J., Ryan, P.G., Sanson, L., Shaw, J.D., Sparrow, M.D., Summerhayes, C., Terauds, A., and Wall, D.H. 2012. Challenges to future conservation of the Antarctic. *Science* 337(6091): 158-159. doi: 10.1126/science.1222821
- Christie, P. 1987. Nitrogen in two contrasting Antarctic bryophyte communities. *Journal of Ecology* 75: 73-93.
- Christner, B.C., Kvitko, B.H., and Reeve, J.N. 2003. Molecular Identification of Bacteria and Eukarya Inhabiting an Antarctic Cryoconite Hole. *Extremophiles* 7: 177-183.
- Clausen, B., and Biggs, B.J.F. 2000. Flow variables for ecological studies in temperate streams: groupings based on covariance. *Journal of Hydrology* 237: 184-197.
- Conovitz, P.A., McKnight, D.M., MacDonald, L.H., Fountain, A.G., and House, H.R. 1998. Hydrologic processes influencing streamflow variation in Fryxell Basin, Antarctica. In Prisco, J.C., Ed. *Ecosystem Dynamics in a Polar Desert: The McMurdo Dry Valleys, Antarctica*, Antarctic Research Series Vol. 72. Washington, D.C.: American Geophysical Union, 93-108.
- Convey, P., and Stevens, M.I. 2007. Antarctic biodiversity. *Science* 317: 1877-1878.
- Cozzetto, K.D., Bencala, K.E., Gooseff, M.N., and McKnight, D.M. 2013. The influence of stream thermal regimes and preferential flow paths on hyporheic exchange in a glacial meltwater stream. *Water Resources Research* 49: 1-18.
- Cozzetto, K., McKnight, D., Nylen, T., and Fountain, A. 2006. Experimental investigations into processes controlling stream and hyporheic temperatures, Fryxell Basin, Antarctica. *Advances in Water Resources* 29: 130-153.
- Cullis, J.D., Gillis, C.A., Bothwell, M.L., Kilroy, C., Packman, A., and Hassan, M. 2012. A conceptual model for the blooming behavior and persistence of the benthic mat-forming diatom *Didymosphenia geminata* in oligotrophic streams. *Journal of Geophysical Research: Biogeosciences* (2005–2012) 117: G2.
- Cullis, J.D.S., Stanish, L.F., and McKnight, D.M. 2014. Diel flow pulses drive particulate organic matter transport from microbial mats in a glacial meltwater stream in the McMurdo Dry Valleys. *Water Resources Research* 50. doi:10.1002/2013WR014061.
- Davey, M.C. 1993. Carbon and nitrogen dynamics in a maritime Antarctic stream. *Freshwater Biology* 30: 319–330.

- Davie, A.W., Mitrovic, S.M., and Lim, R.P. 2012. Succession and accrual of benthic algae on cobbles of an upland river following scouring. *Inland Waters* 2: 89-100. doi: 10.5268/IW-2.2.441
- Davis, J.M., Baxter, C.V., Minshall, G.W., Olson, N.F., Tang, C., and Crosby, B.T. 2013. Climate-induced shift in hydrological regime alters basal resource dynamics in a wilderness river ecosystem. *Freshwater Biology* 58: 306-319.
- Des Marais, D.J., and Canfield, D.E. 1994. The carbon isotope biogeochemistry of microbial mats. In Stal, J., and Caumette, P., Eds. *Microbial mats: structure, development, and environmental significance*. NATO-ASI series, VG35. Berlin Heidelberg: Springer-Verlag, 289–298. doi: 10.1007/978-3-642-78991-5_30
- Dodds, W.K., and Biggs, B.J.F. 2002. Water velocity attenuation by stream benthic algae in relation to growth form and architecture. *Journal of the North American Benthological Society* 21: 2-15.
- Dodds, W.K., Collins, S.M., Hamilton, S.K., Tank, J.L., Johnson, S., Webster, J.R., Simon, K.S., Whiles, M.R., Rantala, H.M., McDowell, W.H., Peterson, S.D., Riis, T., Crenshaw, C.L., Thomas, S.A., Kristensen, P.B., Cheever, B.M., Flecker, A.S., Griffiths, N.A., Crowl, T., Rosi-Marshall, E.J., El-Sabaawi, R., and Martí, E. 2014. You are not always what we think you eat: selective assimilation across multiple whole-stream isotopic tracer studies. *Ecology* 95(10): 2757-2767.
- Dodds, W.K., Gido, K.B., Whiles, M.R., Fritz, K.M., and Matthews, W.J. 2004. Life on the edge: the ecology of Great Plains prairie streams. *Bioscience* 54: 205-216.
- Dodds, W.K., Gudder, D.A., and Mollenhauer, D. 1995. The ecology of *Nostoc*. *Journal of Phycology* 31(1): 2-18. doi: 10.1111/j.0022-3646.1995.00002.x
- Doran, P.T., Priscu, J.C., Lyons, W.B., Walsh, J.E., Fountain, A.G., McKnight, D.M., Moorhead, D.L., Virginia, R.A., Wall, D.H., Clow, G.D., Fritsen, C.H., McKay, C.H., and Parsons, A.N. 2002. Antarctic climate cooling and terrestrial ecosystem response. *Nature* 415: 517-520.
- Doran, P.T., McKay, C.P., Fountain, A.G., Nylen, T., McKnight, D.M., Jaros, C., and Barrett, J.E. 2008. Hydrologic response to extreme warm and cold summers in the McMurdo Dry Valleys, East Antarctica. *Antarctic Science* 20(5): 499-509. doi: 10.1017/S0954102008001272
- Doran, P.T., Wharton Jr., R.A., Des Marais, D.J., and McKay, C.P. 1998. Antarctic paleolake sediments and the search for extinct life on Mars. *Journal of Geophysical Research* 103: 28481–28493. doi:10.1029/98JE01713
- Elser, J.J. 2003. Biological stoichiometry: a theoretical framework connecting ecosystem ecology, evolution, and biochemistry for application in astrobiology. *International Journal of Astrobiology* 2(3): 185-193. doi: 10.1017/S1473550403001563

- Elser, J.J., Watts, J., Schampel, J.H., and Farmer, J. 2006. Early Cambrian food webs on a trophic knife-edge? A hypothesis and preliminary data from a modern stromatolite-based ecosystem. *Ecology Letters* 9: 295-303. doi: 10.1111/j.1461-0248.2005.00873.x
- Esposito, R.M.M., Horn, S.L., McKnight, D.M., Cox, M.J., Grant, M.C., Spaulding, S.A., Doran, P.T., and Cozzetto, K.D. 2006. Antarctic climate cooling and response of diatoms in glacial meltwater streams. *Geophysical Research Letters* 33(7): L07406.1-L07406.4. doi: 10.1029/2006GL025903.
- Esposito, R.M.M., Spaulding, S.A., McKnight, D.M., Van De Vijver, B., Kopalová, K., Lubinski, D., Hall, B., and Whittaker, T. 2008. Inland diatoms from the McMurdo Dry Valleys and James Ross Island, Antarctica. *Canadian Journal of Botany* 86: 1378-1392. doi: 10.1139/B08-100.
- Finlay, J.C. 2004. Patterns and controls of lotic algal stable carbon isotope ratios. *Limnology and Oceanography* 49: 850–61.
- Finlay, J.C., and Kendall, C. 2007. Stable isotope tracing of temporal and spatial variability in organic matter sources to freshwater ecosystems, In Michener, R., and Lajtha, K., Eds. *Stable isotopes in ecology and environmental science*, 2nd ed. Oxford, UK: Blackwell Publishing, 283-333.
- Finlay, J.C., Power, M.E., and Cabana, G. 1999. Effects of water velocity on algal carbon isotope ratios: Implications for river food web studies. *Limnology and Oceanography* 44: 1198-1203.
- Fisher, S.G., Gray, L.J., Grimm, N.B., and Busch, D.E. 1982. Temporal succession in a desert stream ecosystem following flash flooding. *Ecological Monographs* 52: 93-110.
- Foreman, C.M., Wolf, C.F., and Priscu, J.C. 2004. Impact of episodic warming events on the physical, chemical, and biological relationships of lakes in the McMurdo Dry Valleys, Antarctica. *Aquatic Geochemistry* 10: 239-268.
- Fountain, A.G., Levy, J.S., Gooseff, M.N., and Van Horn, D. 2014. The McMurdo Dry Valleys: a landscape on the threshold of change. *Geomorphology* 225: 25-35. doi:10.1016/j.geomorph.2014.03.044
- Fountain, A.G., Lyons, W.B., Burkins, M.B., Dana, G.L., Doran, P.T., Lewis, K.J., McKnight, D.M., Moorhead, D.L., Parsons, A.N., Priscu, J.C., Wall, D.H., Wharton, R.A., and Virginia, R.A. 1999. Physical controls on the Taylor Valley ecosystem, Antarctica. *Bioscience* 49(12): 961-971.
- Francoeur, S.N., and Biggs, B.J.F. 2006. Short-term effects of elevated velocity and sediment abrasion on benthic algal communities. *Hydrobiologia* 561: 59-69.

- Fritsch, F.E. 1912. Freshwater algae. National Antarctic “Discovery” Expedition 1901-1904. British Museum of Natural History 6: 1-66.
- Fritz, K.M., and Dodds, W.K. 2005. Harshness: characterisation of intermittent stream habitat over space and time. *Marine and Freshwater Research* 56: 13-23.
- Fuller, F.L., Doyle, S., Levy, L., Owens, J., Shope, E., Vo, L., Wolyniak, E., Small, M.J., and Doyle, M.W. 2011. Impact of regulated releases on periphyton and macroinvertebrate communities: the dynamic relationship between hydrology and geomorphology in frequently flooded rivers. *River Research and Applications* 27: 630-645.
- Garland, D.D. 2013. Influences of temperature on antarctic freshwater diatom growth rates in culture. Master’s Thesis, University of Colorado.
- Gooseff, M.N., Barrett, J.E., and Levy, J.S. 2013. Shallow groundwater systems in a polar desert, McMurdo Dry Valleys, Antarctica. *Hydrogeology Journal* 21: 171–183. doi: 10.1007/s10040-012-0926-3
- Gooseff, M.N., McKnight, D.M., Carr, M.H., and Baeseman, J. 2010. Antarctic McMurdo Dry Valley stream ecosystems as an analog to fluvial systems on Mars. In Doran, P.T., Lyons, W.B., and McKnight, W.B., Eds. *Life in Antarctic deserts and other cold dry environments*. Cambridge, UK: Cambridge University Press, 139-159.
- Gooseff, M.N., McKnight, D.M., Doran, P., Fountain, A.G., and Lyons, W.B. 2011. Hydrological connectivity of the landscape of the McMurdo Dry Valleys, Antarctica. *Geography Compass* 5/9: 666-681. doi: 10.1111/j.1749-8198.2011.00445.x
- Gooseff, M.N., McKnight, D.M., Lyons, W.B., and Blum, A.E. 2002. Weathering reactions and hyporheic exchange controls on stream water chemistry in a glacial meltwater stream in the McMurdo Dry Valleys. *Water Resources Research* 38(12): 15-1.
- Gooseff, M.N., McKnight, D.M., Runkel, R.L., and Duff, J.H. 2004. Denitrification and hydrologic transient storage in a glacial meltwater stream, McMurdo Dry Valleys, Antarctica. *Limnology and Oceanography* 49(5): 1884-1895.
- Gooseff, M.N., McKnight, D.M., Runkel, R.L., and Vaughn, B.H. 2003. Determining long time-scale hyporheic zone flow paths in Antarctic streams. *Hydrological Processes* 17: 1691-1710.
- Green, W.J., Angle, M.P., and Chave, K.E. 1988. The geochemistry of Antarctic streams and their role in the evolution of four lakes in the McMurdo Dry Valleys. *Geochimica et Cosmochimica Acta* 52: 1265-1274.
- Green, W.J., Stage, B.R., Preston, A., Wagers, S., Shacat, J., and Newell, S. 2005. Geochemical processes in the Onyx River, Wright Valley, Antarctica: Major ions, nutrients, trace metals. *Geochimica et Cosmochimica Acta* 69(4): 839–850. doi:10.1016/j.gca.2004.08.001

- Grimm, N.B., and Fisher, S.G. 1989 Stability of periphyton and macroinvertebrates to disturbance by flash floods in a desert stream. *Journal of the North American Benthological Society* 8: 293–307.
- Hage, M.M., Uhle, M.E., and Macko, S. 2007. Biomarker and stable isotope characterization of coastal pond-derived organic matter, McMurdo Dry Valleys, Antarctica. *Astrobiology* 7(4): 645-661. doi: 10.1089/ast.2006.0033
- Hanson, D.T., Collins, A.M., Jones, H.D., Roesgen, J., Lopez-Nieves, S., and Timlin, J.A. 2014. On-line stable isotope gas exchange reveals an inducible but leaky carbon concentrating mechanism in *Nannochloropsis salina*. *Photosynthesis research* 121(2-3): 311-322.
- Harrell Jr, F.E., and Dupont, C. 2014. Hmisc: Harrell Miscellaneous. R package version 3.14-5. Available at <http://cran.r-project.org/web/packages/Hmisc/index.html>. Accessed 26 Oct 2014.
- Hart, D.D., Biggs, B.J.F., Nikora, V.I., and Flinders, C.A. 2013. Flow effects on periphyton patches and their ecological consequences in a New Zealand river. *Freshwater Biology* 58: 1588-1602.
- Hawes, I. 1989. Filamentous green algae in freshwater streams on Signy Island, Antarctica. *Hydrobiologia* 172: 1-18.
- Hawes, I., and Brazier, P. 1991. Freshwater stream ecosystems of James Ross Island, Antarctica. *Antarctic Science* 3: 265–271.
- Hawes, I., and Howard-Williams, C. 1998. Primary production processes in streams of the McMurdo Dry Valleys, Antarctica. In Prisco, J.C., Ed. *Ecosystem Dynamics in a Polar Desert: The McMurdo Dry Valleys, Antarctica*, Antarctic Research Series Vol. 72. Washington, D.C.: American Geophysical Union, 129–140.
- Hawes, I., Howard-Williams, C., and Sorrell, B. 2014. Decadal timescale variability in ecosystem properties in the ponds of the McMurdo Ice Shelf, southern Victoria Land, Antarctica. *Antarctic Science* 26(3): 219-230. doi: 10.1017/S0954102013000576
- Hawes, I., Howard-Williams, C., and Vincent, W.F. 1992. Desiccation and recovery of Antarctic cyanobacterial mats. *Polar Biology* 12: 587-594.
- Hawes, I., Smith, R., and Sutherland, D. 1999. Development of microbial mats on contaminated soils from the former site of Vanda Station, Antarctica. *New Zealand Natural Sciences* 24: 53-68.
- Hawes, I., Sumner, D.Y., Andersen, D.T., Jungblut, A.D., and Mackey, T.J. 2013. Timescales of Growth Response of Microbial Mats to Environmental Change in an Ice-Covered Antarctic Lake. *Biology* 2: 151-176. doi:10.3390/biology2010151

- Hedges, J.I., and Stern, J.H. 1984. Carbon and nitrogen determinations of carbonate containing solids. *Limnology and Oceanography* 29: 657-663. doi: 10.4319/lo.1984.29.3.0657
- Hill, B.H., Elonen, C.M., Seifert, L.R., May, A.A., and Tarquinio, E. 2012. Microbial enzyme stoichiometry and nutrient limitation in US streams and rivers. *Ecological Indicators* 18: 540–551.
- Hill, W.R., Fanta, S.E., and Roberts, B.J. 2008. ¹³C dynamics in benthic algae: Effects of light, phosphorus, and biomass development. *Limnology and Oceanography* 53(4): 1217–1226. doi: 10.4319/lo.2008.53.4.1217.
- Hillebrand, H., Dürselen, C., Kirschtel, D., Pollinger, U., and Zohary, T. 1999. Biovolume calculation for pelagic and benthic microalgae. *Journal of Phycology* 35: 403–424.
- Hobbie, J.E., Peterson, B.J., Bettez, N., Deegan, L., O'Brien, W.J., Kling, G.W., Kipphut, G.W., Bowden, W.B., and Hershey, A.E. 1999. Impact of global change on the biogeochemistry and ecology of an Arctic freshwater system. *Polar Research* 18: 207-214. doi: 10.1111/j.1751-8369.1999.tb00295.x
- Hoehler, T.M., Bebout, B.M., and Des Marais, D.J. 2001. The role of microbial mats in the production of reduced gases on the early Earth. *Nature* 412(6844): 324-327.
- House, H.R., McKnight, D.M., and von Guerard, P. 1995. The influence of stream channel characteristics on stream flow and annual water budgets for lakes in Taylor Valley. *Antarctic Journal of the United States*. 30: 284-287.
- Howard-Williams, C., and Hawes, I. 2007. Ecological processes in Antarctic inland waters: interactions between physical processes and the nitrogen cycle. *Antarctic Science* 19(2): 205-217. doi: 10.1017/S0954102007000284
- Howard-Williams, C., Hawes, I., Schwarz, A.-M., and Hall, J.A. 1997. Sources and sinks of nutrients in a polar desert stream, the Onyx River, Antarctica. In Lyons, W.B., Howard-Williams, C., and Hawes, I., Eds. *Ecosystem Processes in Antarctic Ice-Free Landscapes*. Rotterdam, Netherlands: Balkema Press, 155-170.
- Howard-Williams, C., Priscu, J.C., and Vincent, W.F. 1989. Nitrogen dynamics in two Antarctic streams. *Hydrobiologia* 172: 51-61.
- Howard-Williams, C., Vincent, C.L., Broady, P.A., and Vincent, W.F. 1986. Antarctic stream ecosystems: Variability in environmental properties and algal community structure. *Internationale Revue der Gesamten Hydrobiologie und Hydrographie* 71: 511–544.
- Huiskes, A.H.L., Gremmen, N.J.M., Bergstrom, D.M., Frenot, Y., Hughes, K.A., Imura, S., Kiefer, K., Lebouvier, M., Lee, J.E., Tsujimoto, M., Ware, C., Van de Vijver, B., and Chown, S.L. 2014. Aliens in Antarctica: Assessing transfer of plant propagules by human visitors to reduce invasion risk. *Biological Conservation* 171: 278-284.

- Humphries, P., Keckeis, H., and Finlayson, B. 2014. The River Wave Concept: Integrating river ecosystem models. *BioScience* 64: 870-882. doi: 10.1093/biosci/biu130
- Huntington, T.G. 2006. Evidence for intensification of the global water cycle: Review and synthesis. *Journal of Hydrology* 319: 83-95.
- Huryn, A.D., Slavik, K.A., Lowe, R.L., Parker, S.M., Anderson, D.S., and Peterson, B.J. 2005. Landscape heterogeneity and the biodiversity of Arctic stream communities: a habitat template analysis. *Canadian Journal of Fisheries and Aquatic Sciences* 62: 1905-1919.
- Izaguirre, I., and Pizarro, H. 1998. Epilithic algae in a glacial stream at Hope Bay (Antarctica). *Polar Biology* 19: 24-31.
- John, D.M. 2003. Filamentous and plantlike green algae. In Wehr, J.D., and Sheath, R.G., Eds. *Freshwater algae of North America: Ecology and classification*. San Diego, CA: Academic Press, 311-352.
- John, D.M., Whitton, B.A., and Brook, A.J. 2002. *The Freshwater Algal Flora of the British Isles: An identification guide to freshwater and terrestrial algae*. Cambridge, UK: Cambridge University Press and The Natural History Museum, 702.
- Jaros, C.L. 2003. Temperature-elevation effect on glacial meltwater generation in dry valley streams, Antarctica. Master's Thesis, University of Colorado.
- Jones, C.G., Lawton, J.H., and Shachak, M. 1994. Organisms as ecosystem engineers. *Oikos* 69(3): 373-386.
- Junk, W.J., Bayley, P.B., and Sparks, R.E. 1989. The flood pulse concept in river-floodplain systems. *Canadian Special Publication of Fisheries and Aquatic Sciences* 106: 110-127.
- Keeley, J.E., and Sandquist, D.R. 1992. Carbon: freshwater plants. *Plant, Cell and Environment* 15(9): 1021-1035.
- Kemp, M.J., and Dodds, W.K. 2001. Spatial and temporal patterns of nitrogen concentrations of pristine and agriculturally-influenced prairie streams. *Biogeochemistry* 53: 125-141.
- Kennicutt II, M.C., Chown, S.L., Cassano, J.J., Liggett, D., Massom, R., Peck, L.S., Rintoul, S.R., Storey, J.W.V., Vaughan, D.G., Wilson, T. J., and Sutherland, W.J. 2014. Polar research: Six priorities for Antarctic science. *Nature* 512: 23-5. doi: 10.1038/512023a
- Koch, J.C., McKnight, D.M., and Baeseman, J.L. 2010. Effect of unsteady flow on nitrate loss in an oligotrophic, glacial meltwater stream, *Journal of Geophysical Research-Biogeosciences*, 115: G01001. doi: 10.1029/2009JG001030

- Koch, J.C., McKnight, D.M., and Neupauer, R.M. 2011. Simulating unsteady flow, anabranching, and hyporheic dynamics in a glacial meltwater stream using a coupled surface water routing and groundwater flow model. *Water Resources Research* 47: W05530.
- Kohler, T.J., Heatherly II, T.N., El-Sabaawi, R.W., Zandonà, E., Marshall, M.C., Flecker, A.S., Pringle, C.M., Reznick, D.N., and Thomas, S.A. 2012. Flow, nutrients and light availability influence Neotropical epilithon biomass and stoichiometry. *Freshwater Science* 31: 1019-1034. doi: 10.1899/11-141.1
- Kohler, T.J., Murdock, J.N., Gido, K.B., and Dodds, W.K. 2011. Nutrient loading and grazing by the minnow *Phoxinus erythrogaster* shift periphyton abundance and stoichiometry in mesocosms. *Freshwater Biology* 56: 1133-1146. doi: 10.1111/j.1365-2427.2010.02557.x
- Komárek, J. 2007. Phenotype diversity of the cyanobacterial genus *Leptolyngbya* in the Maritime Antarctic. *Polish Polar Research* 28(3): 211-231.
- Komárek, J., and Anagnostidis, K. 2005. Cyanoprokaryota - 2. Teil: Oscillatoriales. In Buedel, B., Krienitz, L., Gaertner, G. and Schagerl, M., Eds. *Süßwasserflora von Mitteleuropa*, Band 19/2. Heidelberg: Elsevier/Spektrum, 759.
- Komárek, J., J. Kaštovsky, S. Ventura, S. Turicchia, and J. Šmarda. 2009. The cyanobacterial genus *Phormidesmis*. *Algological Studies* 129: 41-59. doi: 10.1127/1864-1318/2009/0129-0041
- Konfirst, M.A., Sjunneskog, C., Scherer, R.P., and Doran, P.T. 2011. A diatom record of environmental change in Fryxell Basin, Taylor Valley, Antarctica, late Pleistocene to present. *Journal of Paleolimnology* 46: 257-272. doi: 10.1007/s10933-011-9537-6
- Kopalová, K., Kociolek, J.P., Lowe, R.L., Zidarova, R., and Van De Vijver, B. *In press*. Five new species of the genus *Humidophila* (Bacillariophyta) from the Maritime Antarctic Region. *Diatom Research*. doi: 10.1080/0269249X.2014.998714
- Kopalová, K., Nedbalová, L., Nyvlt, D., Elster, J., and Van de Vijver, B. 2013. Diversity, ecology and biogeography of the freshwater diatom communities from Ulu Peninsula (James Ross Island, NE Antarctic Peninsula). *Polar Biology* 36(7): 933-948. doi: 10.1007/s00300-013-1317-5
- Kopalová, K., Ochyra, R., Nedbalová, L., and Van de Vijver, B. 2014. Moss-inhabiting diatoms from two contrasting Maritime Antarctic islands. *Plant Ecology and Evolution* 147(1): 67-84.
- Kopalová, K., and Van de Vijver, B. 2013. Structure and ecology of freshwater benthic diatom communities from Byers Peninsula, Livingston Island, South Shetland Island. *Antarctic Science* 25(2): 239-253. doi: 10.1017/S0954102012000764
- Kopalová, K., Veselá, J., Elster, J., Nedbalová, L., Komárek, J., and Van De Vijver, B. 2012. Benthic diatoms (Bacillariophyta) from seepages and streams on James Ross Island (NW

- Weddell Sea, Antarctica). *Plant Ecology and Evolution* 145: 190-208. doi: 10.5091/plecevo.2012.639
- Kováčik, L., and Pereira, A.B. 2001. Green alga *Prasiola crispa* and its lichenized form *Mastodia tessellata* in Antarctic environment: General aspects. *Nova Hedwigia* 123: 465-478.
- Kumar, S., Spaulding, S.A., Stohlgren, T.J., Hermann, K.A., Schmidt, T.S., and Bahls, L.L. 2009. Potential habitat distribution for the freshwater diatom *Didymosphenia geminata* in the continental US. *Frontiers in Ecology and the Environment* 7: 415-420.
- Kuznetsova, A., Brockhoff, P.B., and Christensen, R.H.B. 2014. lmerTest: Tests for random and fixed effects for linear mixed effect models (lmer objects of lme4 package). R package version 2.0-11. Availailbe: <http://CRAN.R-project.org/package=lmerTest>
- Laws, E.A., Popp, B.N., Bidigare, R.R., Kennicutt, M.C., and Macko, S.A. 1995. Dependence of phytoplankton carbon isotopic composition on growth rate and $[CO_2]_{aq}$: Theoretical considerations and experimental results. *Geochimica et Cosmochimica Acta* 59: 1131-1138.
- Lawson, J., Doran, P.T., Kenig, F., Des Marais, D.J., and Priscu, J.C. 2004. Stable carbon and nitrogen isotopic composition of benthic and pelagic organic matter in lakes of the McMurdo Dry Valleys, Antarctica. *Aquatic Geochemistry* 10: 269-301. doi: 10.1007/s10498-004-2262-2
- Lawson Knoepfle, J., Doran, P.T., Kenig, F., Lyons, W.B., and Galchenko, V. 2009. Particulate organic and dissolved inorganic carbon stable isotopic compositions in Taylor Valley lakes, Antarctica: the effect of legacy. *Hydrobiologia* 632: 139-156.
- Lehmann, M.F., Reichert, P., Bernasconi, S.M., Barbieri, A., and McKenzie, J.A. 2003. Modelling nitrogen and oxygen isotope fractionation during denitrification in a lacustrine redox-transition zone. *Geochimica et Cosmochimica Acta* 67(14): 2529-2542.
- Levy, J.S., Fountain, A.G., Dickson, J.L., Head, J.W., Okal, M., Marchant, D.R., and Watters, J. 2013. Accelerated thermokarst formation in the McMurdo Dry Valleys, Antarctica 3: 2269. doi: 10.1038/srep02269
- Lionard, M., Péquin, B., Lovejoy, C., and Vincent, W.F. 2012. Benthic cyanobacterial mats in the high Arctic: multi-layer structure and fluorescence responses to osmotic stress. *Frontiers in Microbiology* 3(140). doi: 10.3389/fmicb.2012.00140
- Lorenzen, C., and Jeffrey, S. 1980. Determination of chlorophyll in seawater. *UNESCO technical papers in marine science* 35: 1-20.
- Lyons, W.B., Leslie, D.L., Harmon, R.S., Neumann, K., Welch, K.A., Bisson, K.M., and McKnight, D.M. 2013. The carbon stable isotope biogeochemistry of streams, Taylor Valley, Antarctica. *Applied Geochemistry* 32: 26-36.

- Lyons, W.B., Welch, K.A., Carey, A.E., Doran, P.T., Wall, D.H., Virginia, R.A., Fountain, A.G., Csathó, B.M., and Tremper, C.M. 2005. Groundwater seeps in Taylor Valley, Antarctica: an example of a subsurface melt event. *Annals of Glaciology* 40: 200-206. doi: 10.3189/172756405781813609
- Maestrel, F.T., Callaway, R.M., Valladares, F., and Lortie, C.J. 2009. Refining the stress-gradient hypothesis for competition and facilitation in plant communities. *Journal of Ecology* 97(2): 199-205. doi: 10.1111/j.1365-2745.2008.01476.x
- Maurice, P.A., McKnight, D.M., Gooseff, M.N., Leff, L., and Fulghum, J.E. 2002. Direct observations of aluminosilicate weathering in the hyporheic zone of an Antarctic dry valley stream. *Geochimica et Cosmochimica Acta* 66: 1335-1347.
- McGinnis, L.D., and Jensen, T.E. 1971. Permafrost-hydrogeologic regimen in two ice-free valleys, Antarctica, from electrical depth sounding. *Quaternary Research* 1(3): 389-409. doi:10.1016/0033-5894(71)90073-1
- McIntyre, P.B., Flecker, A.S., Vanni, M.J., Hood, J.M., Taylor, B.W., and Thomas, S.A. 2008. Fish distributions and nutrient cycling in streams: Can fish create biogeochemical hotspots? *Ecology* 89: 2335-2346.
- McKnight, D.M., Alger, A.S., Tate, C.M., Shupe, G., and Spaulding, S. 1998. Longitudinal patterns in algal abundance and species distribution in meltwater streams in Taylor Valley, Southern Victoria Land, Antarctica. In Prisco, J.C., Ed. *Ecosystem Dynamics in a Polar Desert: The McMurdo Dry Valleys, Antarctica*, Antarctic Research Series Vol. 72. Washington, D.C.: American Geophysical Union, 109-127.
- McKnight, D.M., and Andrews, E.D. 1993. Potential hydrologic and geochemical consequences of the 1992 merging of Lake Chad with Lake Hoare in Taylor Vally. *Antarctic Journal* 249-251.
- McKnight, D.M., Niyogi, D.K., Alger, A.S., Bomblies, A., Conovitz, P.A., and Tate, C.M. 1999. Dry Valley Streams in Antarctica: ecosystems waiting for water. *BioScience* 49(12): 985-995.
- McKnight, D.M., Runkel, R.L., Tate, C.M., Duff, J.H., and Moorhead, D.L. 2004. Inorganic N and P dynamics of Antarctic glacial meltwater streams as controlled by hyporheic exchange and benthic autotrophic communities. *Journal of the North American Benthological Society*. 23: 171-188.
- McKnight, D.M., and Tate, C.M. 1997. Canada Stream: A glacial meltwater stream in Taylor Valley, South Victoria Land, Antarctica. *Journal of the North American Benthological Society* 16: 14-17.
- McKnight, D.M., Tate, C.M., Andrews, E.D., Niyogi, D.K., Cozzetto, K., Welch, K., Lyons, W.B., and Capone, D.G. 2007. Reactivation of a cryptobiotic stream ecosystem in the

- McMurdo Dry Valleys, Antarctica: A long-term geomorphological experiment. *Geomorphology* 89: 186-204.
- Michalski, G., Bockheim, J.G., Kendall, C., and Thiemens, M. 2005. Isotopic composition of Antarctic Dry Valley nitrate: Implications for NO_y sources and cycling in Antarctica. *Geophysical Research Letters* 32: L13817. doi: 10.1029/2004GL022121.
- Michaud, A.B., Šabacká, M. and Priscu, J.C. 2012. Cyanobacterial diversity across landscape units in a polar desert: Taylor Valley, Antarctica. *FEMS Microbiology Ecology* 82(2): 268-278. doi: 10.1111/j.1574-6941.2012.01297.x
- Michener, R., and Lajtha, K. 2007. *Stable isotopes in ecology and environmental science*, 2nd ed. Oxford, UK: Blackwell Publishing, 566 pp.
- Miller, M.P., McKnight, D.M., Cullis, J.D., Greene, A., Vietti, K., and Liptzin, D. 2009. Factors controlling streambed coverage of *Didymosphenia geminata* in two regulated streams in the Colorado Front Range. *Hydrobiologia* 630: 207-218.
- Moniz, M.B.J., Rindi, F., Novis, P.M., Broady, P.A., and Guiry, M.D. 2012. Molecular phylogeny of Antarctic *Prasiola* (Prasiolales, Trebouxiophyceae) reveals extensive cryptic diversity. *Journal of Phycology* 48: 940-955. doi: 10.1111/j.1529-8817.2012.01172.x
- Montoya, J.P., and McCarthy, J.J. 1995. Isotopic fractionation during nitrate uptake by phytoplankton grown in continuous culture. *Journal of Plankton Research* 17(3): 439-464.
- Morgan-Kiss, R.M., Priscu, J.C., Pocock, T., Gudynaite-Savitch, L., and Huner, N.P.A. 2006. Adaptation and acclimation of photosynthetic microorganisms to permanently cold environments. *Microbiology and Molecular Biology Reviews* 70: 222-252. doi: 10.1128/MMBR.70.1.222-252.2006
- Mueller, D.R., and Vincent, W.F. 2006. Microbial habitat dynamics and ablation control on the Ward Hunt Ice Shelf. *Hydrologic Processes* 20: 857-876. doi: 10.1002/hyp.6113
- Murphy, J., and Riley, J.P. 1962. A modified single solution method for determination of phosphate in natural waters. *Analytica Chimica Acta* 26: 31-36.
- Needoba, J.A., Waser, N.A., Harrison, P.J., and Calvert, S.E. 2003. Nitrogen isotope fractionation in 12 species of marine phytoplankton during growth on nitrate. *Marine Ecology Progress Series* 255: 81-91.
- Neumann, K., Lyons, W.B., and Des Marais, D.J. 1998. Inorganic carbon-isotope distribution and budget in the Lake Hoare and Fryxell basins, Taylor Valley, Antarctica. *Annals of Glaciology* 27: 685-690.

- Nielsen, U.N., Wall, D.H., Adams B.J., Virginia R.A., Ball, B.A., Gooseff, M.N., and McKnight, D.M. 2012. The ecology of pulse events: insights from an extreme climatic event in a polar desert ecosystem. *Ecosphere* 3(2): 17. doi: 10.1890/ES11-00325.1
- Niyogi, D.K., Tate, C.M., McKnight, D.M., Duff, J.H., and Alger, A.S. 1997. Species composition and primary production of algal communities in Dry Valley streams in Antarctica: Examination of the functional role of biodiversity. In Lyons WB, Howard Williams C, Hawes I, Eds. *Ecosystem processes in Antarctic ice-free landscapes*. Rotterdam: Balkema, 171-179.
- Nkem, J.N., Wall, D.H., Virginia, R.A., Barrett, J.E., Broos, E.J., Porazinska, D.L., and Adams, B.J. 2006. Wind Dispersal of Soil Invertebrates in the McMurdo Dry Valleys, Antarctica. *Polar Biology* 29: 346-352.
- Nylen, T.H., Fountain, A.G., and Doran, P.T. 2004. Climatology of katabatic winds in the McMurdo Dry Valleys, southern Victoria Land, Antarctica. *Journal of Geophysical Research-Atmospheres* 109(D3): D03114.
- Ohtani, S., Suvama, K., and Kanda, H. 2000. Environmental monitoring by means of soil algae and microorganisms in the vicinity of Syowa Station. *Nankyoku Shiryo (Antarctic Record)* 44: 265-276.
- O'Neill, T.A., Balks, M.R., and López-Martínez, J. 2013. Visual recovery of desert pavement surfaces following impacts from vehicle and foot traffic in the Ross Sea region of Antarctica. *Antarctic Science* 25(4): 514-530. doi:10.1017/S0954102012001125
- Otero, A., and Vincenzini, M. 2004. *Nostoc* (Cyanophyceae) goes nude: extracellular polysaccharides serve as a sink for reducing power under unbalanced C/N metabolism. *Journal of Phycology* 40: 74-81. doi: 10.1046/j.1529-8817.2004.03067.x
- Paerl, H.W., Pinckney, J.L., and Steppe, T.F. 2000. Cyanobacterial-bacterial mat consortia: examining the functional unit of microbial survival and growth in extreme environments. *Environmental Microbiology* 2(1): 11-26.
- Papineau, D., Walker, J.J., Mojzsis, S.J., and Pace, N.R. 2005. Composition and structure of microbial communities from stromatolites of Hamelin Pool in Shark Bay, Western Australia. *Applied and Environmental Microbiology* 71(8): 4822. doi: 10.1128/AEM.71.8.4822-4832.2005.
- Parker, S.M., and Huryn, A.D. 2011. Effects of natural disturbance on stream communities: a habitat template analysis of arctic headwater streams. *Freshwater Biology* 56: 1342-1357.
- Peipoch, M., Gacia, E., Pastor, A., Ribot, M., Riera, J.Ll., Sabater, F., and Martí, E. 2014. Intrinsic and extrinsic drivers of autotrophic nitrogen cycling in stream ecosystems: Results

- from a translocation experiment. *Limnology and Oceanography* 59(6): 1973-1986. doi: 10.4319/lo.2014.59.6.1973
- Pertierra, L.R., Lara, F., Tejedro, P., Quesada, A., and Benayas, J. 2013. Rapid denudation processes in cryptogamic communities from Maritime Antarctica subjected to human trampling. *Antarctic Science* 25: 318-328. doi: 10.1017/S095410201200082X
- Peterson, B.J., Bahr, M., and Kling, G.W. 1997. A tracer investigation of nitrogen cycling in a pristine tundra river. *Canadian Journal of Fisheries and Aquatic Sciences* 54(10): 2361-2367.
- Peterson, B.J., and Fry, B. 1987. Stable isotopes in ecosystem studies. *Annual Review of Ecology and Systematics* 18: 293-320.
- Pinheiro, J., Bates, D., Debroy, S., and Sarkar, D. 2006. nlme: an R package for fitting and comparing Gaussian linear and nonlinear mixed-effects models. R project for statistical computing, Vienna, Austria. Available: <http://www.stats.bris.ac.uk/R/>
- Pizarro, H., and Vincour, A. 2000. Epilithic biomass in an outflow stream at Potter Peninsula, King George Island, Antarctica. *Polar Biology* 23: 851-857.
- Pla-Ribes, S., Toro, M., Van de Vijver, B., Rochera, C., Villaescusa, J.A., Camacho, A., and Quesada, A. 2013. Stability and endemism of benthic diatom assemblages from different substrates in a maritime stream on Byers Peninsula, Livingston Island, Antarctica: the role of climate variability. *Antarctic Science* 25(2): 254-269. doi: 10.1017/S0954102012000922
- Poff, N.L., Allen, J.D., Bain, M.B., Karr, J.R., Prestegard, K.L., Richter, B.D., Sparks, R.E., and Stromberg, J.C. 1997. The natural flow regime: A paradigm for river conservation and restoration. *Bioscience* 47: 769-784.
- Poff, N.L., Olden, J.D., Merritt, D.M., and Pepin, D.M. 2007. Homogenization of regional river dynamics by dams and global biodiversity implications. *Proceedings of the National Academy of Sciences* 104: 5732-5737.
- Porazinska, D.L., Fountain, A.G., Nylen, T.H., Tranter, M., Virginia, R.A., and Wall, D.H. 2004. The Biodiversity and Biogeochemistry of Cryoconite Holes from McMurdo Dry Valley Glaciers, Antarctica. *Arctic Antarctic and Alpine Research* 36: 84-91.
- Potts, M. 2000. *Nostoc*. In Whitton, B.A., and Potts, M., Eds. *The ecology of cyanobacteria: their diversity in time and space*. Dordrecht, Netherlands: Kluwer Academic Press, 465-504.
- Priscu, J.C. 1995. Phytoplankton nutrient deficiency in lakes of the McMurdo Dry Valleys, Antarctica. *Freshwater Biology* 34: 215-227.
- Quayle, W.C., Peck, L.S., Peat, H., Ellis-Evans, J.C., and Harrigan, P.R. 2002. Extreme responses to climate change in Antarctic lakes. *Science* 295: 645. doi: 10.1126/science.1064074

- Quesada, A., Fernández-Valiente, E., Hawes, I., and Howard-Williams, C. 2008. Benthic primary production in polar lakes and rivers. In Vincent, W.F., and Laybourn-Parry, J., Eds. *Polar Lakes and Rivers: Limnology of Arctic and Antarctic Aquatic Ecosystems*. New York, NY: Oxford University Press, 179-196.
- R Core Team. 2014. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>.
- Richard, Y., Rouault, M., Pohl, B., Crétat, J., Duclot, I., Taboulot, S., Reason, C.J.C., Macron, C., and Buiron, D. 2013. Temperature changes in the mid- and high- latitudes of the Southern Hemisphere. *International Journal of Climatology* 33: 1948-1963.
- Richard, Y., Rouault, M., Pohl, B., Crétat, J., Duclot, I., Taboulot, S., Reason, C.J.C., Macron, C., and Buiron, D. 2013. Temperature changes in the mid- and high- latitudes of the Southern Hemisphere. *International Journal of Climatology* 33: 1948-1963.
- Roberts, D., and McMinn, A. 1996. Relationships between surface sediment diatom assemblages and water chemistry gradients in saline lakes of the Vestfold Hills, Antarctica. *Antarctic Science* 8(4): 331-341.
- Rochera, C., Fernandez-Valiente, E., Van de Vijver, B., Rico, E., Toro, M., Vincent, W.F., Quesada, A., and Camacho, A. 2013. Community structure and photosynthetic activity of benthic biofilms from a waterfall in the maritime Antarctica. *Polar Biology* 36: 1709-1722. doi: 10.1007/s00300-013-1388-3
- Rouse, W.R., Douglas, M.S.V., Hecky, R.E. Hershey, A.E., Kling, G.W., Lesack, L., Marsh, P., McDonald, M., Nicholson, B.J., Roulet, N.T., and Smol, J.P. 1997. Effects of climate change on the freshwaters of arctic and subarctic North America. *Hydrological Processes* 11: 873–902. doi: 10.1002/(SICI)1099-1085(19970630)11:8<873::AID-HYP510>3.0.CO;2-6
- Royall, R.M. 1997. *Statistical evidence: a likelihood paradigm*. New York, NY: Chapman and Hall.
- Runkel, R.L., McKnight, D.M., and Andrews, E.D. 1998. Analysis of transient storage subject to unsteady flow: diel flow variation in an Antarctic stream. *Journal of the North American Benthological Society* 17: 143-154.
- Šabacká, M., Priscu, J.C., Basagic, H.J., Fountain, A.G., Wall, D.H., Virginia, R.A., and Greenwood, M.C. 2012. Aeolian flux of biotic and abiotic material in Taylor Valley, Antarctica. *Geomorphology* 155-156: 102-111. doi: 10.1016/j.geomorph.2011.12.009
- Sakaeva, A. 2014. Ecology and biogeography of freshwater diatoms in ponds of McMurdo Dry Valleys and parts of the Ross Island. Master's Thesis, University of Colorado.

- Schade, J.D., MacNeill, K., Thomas, S.A., McNeely, F.C., Welter, J.R., Hood, J., Goodrich, M., Power, M.E., and Finlay, J.C. 2011. The stoichiometry of nitrogen and phosphorus spiraling in heterotrophic and autotrophic streams. *Freshwater Biology* 56: 424-436. doi:10.1111/j.1365-2427.2010.02509.x
- Schirrmeister, B.E., de Vos, J.M., Antonellic, A., and Bagheri, H.C. 2013. Evolution of multicellularity coincided with increased diversification of cyanobacteria and the Great Oxidation Event. *Proceedings of the National Academy of Sciences* 110(5): 1791-1796. doi: 10.1073/pnas.1209927110
- Schouten, S., Hartgers, W., Lopez, J., Grimalt, J., and Damste, J. 2001. A molecular isotopic study of ^{13}C -enriched organic matter in evaporitic deposits: recognition of CO_2 -limited ecosystems. *Organic Geochemistry* 32: 277–286. doi: 10.1016/S0146-6380(00)00177-7
- Seaburg, K.G., Parker, B.C., Prescott, G.W., and Whitford, L.A. 1979. The algae of southern Victoria Land. *Bibliotheca Phycologia* 46: 169.
- Simon, K.S., Townsend, C.R., Biggs, B.J.F., and Bowden, W.B. 2004. Temporal variation of N and P uptake in 2 New Zealand streams. *Journal of the North American Benthological Society* 24: 1-18.
- Smeller, J.M. 1995. Comparison of sample preparation methods for the spectrophotometric determination of phosphorus in soil and cola fly ash. *Analyst* 120: 207-210.
- Souffreau, C., Vanormelingen, P., Van de Vijver, B., Isheva, T., Verleyen, E., Sabbe, K., and Vyverman, W. 2013. Molecular Evidence for Distinct Antarctic Lineages in the Cosmopolitan Terrestrial Diatoms *Pinnularia borealis* and *Hantzschia amphioxys*. *Protist* 164(1): 101-115. doi: 10.1016/j.protis.2012.04.001
- Spaulding, S., and Elwell, L. 2007. Increase in nuisance blooms and geographic expansion of the freshwater diatom *Didymosphenia geminata*. Open-File Report 2007-1425. U.S. Geological Survey.
- Spaulding, S.A., McKnight, D.M., Stoermer, E.F., and Doran, P.T. 1997. Diatoms in sediments of perennially ice-covered Lake Hoare, and implications for interpreting lake history in the McMurdo Dry Valleys of Antarctica. *Journal of Paleolimnology* 17: 403-420.
- Spaulding, S., Van de Vijver, B., Hodgson, D., McKnight, D., Verleyen, E., and Stanish, L. 2010. Diatoms as indicators of environmental change in Antarctic and subantarctic freshwaters. In Smol, J.P., and Stoermer, E.F., Eds. *The diatoms: applications for the environmental and earth sciences*, 2nd ed. Cambridge, UK: Cambridge University Press, 267-286.
- Speirs, J.C., Steinhoff, D.F., McGowan, H.A., Bromwich, D.H., and Monaghan, A.J. 2010. Foehn Winds in the McMurdo Dry Valleys, Antarctica: The Origin of Extreme Warming Events. *Journal of Climate* 23: 3577-3598. doi: 10.1175/2010JCLI3382.1

- Speirs, J.C., McGowan, H.A., Steinhoff, D.F., and Bromwich, D.H. 2013. Regional climate variability driven by foehn winds in the McMurdo Dry Valleys, Antarctica. *International Journal of Climatology* 33: 945-958. doi: 10.1002/joc.3481
- Stal, L. J. 2000. Cyanobacterial mats and stromatolites. In Whitton, B.A. and Potts, M., Eds. *The ecology of cyanobacteria: their diversity in time and space*. Dordrecht, Netherlands: Kluwer Academic Press, 61-120.
- Stanish, L.F., Bagshaw, E.A., McKnight, D.M., Fountain, A.G., and Tranter, M. 2013. Environmental factors influencing diatom communities in Antarctic cryoconite holes. *Environmental Research Letters* 8: 045006. doi: 10.1088/1748-9326/8/4/045006
- Stanish, L.F., Kohler, T.J., Esposito, R.M.M., Simmons, B.L., Nielsen, U.N., Wall, D.H., Nemergut, D.R., and McKnight, D.M. 2012. Extreme streams: flow intermittency as a control on diatom communities in meltwater streams in the McMurdo Dry Valleys, Antarctica. *Canadian Journal of Fisheries and Aquatic Sciences* 69(8): 1405-1419. doi: 10.1139/f2012-022
- Stanish, L.F., Nemergut, D.R., and McKnight, D.M. 2011. Hydrologic processes influence diatom community composition in Dry Valley streams. *Journal of the North American Benthological Society* 30: 1057-1073. doi: 10.1899/11-008.1
- Stanish, L.F., O'Neill, S.P., Gonzalez, A., Legg, T.M., Knelman, J., McKnight, D.M., Spaulding, S.A., and Nemergut, D.R. 2012. Bacteria and diatom co-occurrence patterns in microbial mats from polar desert streams. *Environmental Microbiology* 15(4): 1115-1131. doi: 10.1111/j.1462-2920.2012.02872.x
- Stanish, L.F., and Spear, J.R. 2013. Diatom ecology and microbial mat structure and function in Antarctic Dry Valleys. *Palaios* 28(5): 267-269. doi: 10.2110/palo.2013.S03
- Stanley, E.H., Fisher, S.G., and Jones Jr, J.B. 2004. Effects of water loss on primary production: A landscape-scale model. *Aquatic Sciences* 66: 130-138. doi: 10.1007/s00027-003-0646-9
- Steinman, A., Lamberti, G.A., and Leavitt, P.R. 1996. Biomass and pigments of benthic algae. In Hauer, F.R., and Lamberti, G.A., Eds. *Methods in stream ecology*. 2nd ed. San Diego, CA: Academic Press, 357-379.
- Sterner, R.W., and Elser, J.J. 2002. *Ecological stoichiometry: the biology of elements from molecules to the biosphere*. Princeton, NJ: Princeton University Press, 439 pp.
- Stevenson, R.J. 1996. The stimulation and drag of current. In Stevenson, R.J., Bothwell, M.L., and Lowe, R.L., Eds. *Algal ecology: freshwater benthic ecosystems*. San Diego, CA: Academic Press, 321-340.

- Strickland, J.D.H., and Parsons, T.R. 1972. A practical handbook of seawater analysis, 2nd ed. Ottawa, Ontario: Fisheries Research Board of Canada Bulletin, 167.
- Strunecký, O., Elster, J., and Komárek, J. 2012. Molecular clock evidence for survival of Antarctic cyanobacterial (*Oscillatoriales*, *Phormidium autumnale*) from Paleozoic times. FEMS Microbiology Ecology 82: 482-490. doi: 10.1111/j.1574-6941.2012.01426.x
- Strunecký, O., Komárek, J., Johansen, J., Lukešová, A., and Elster, J. 2013. Molecular and morphological criteria for revision of the genus *Microcoleus* (*Oscillatoriales*, cyanobacteria). Journal of Phycology 49: 1167–1180. doi: 10.1111/jpy.12128
- Tanabe, Y., Ohtani, S., Kasamatsu, N., Fukuchi, M., and Kudoh, S. 2010. Photophysiological responses of phytobenthic communities to the strong light and UV in Antarctic shallow lakes. Polar Biology 33: 85-100.
- Tang, E.P.Y., Tremblay, R., and Vincent, W.F. 1997. Cyanobacterial dominance of polar freshwater ecosystems: are high-latitude mat-formers adapted to low temperature? Journal of Phycology 33: 171-181.
- Taton, A., Grubisic, S., Balthasart, P., Hodgson, D.A., Laybourn-Parry, J., and Wilmotte, A. 2006. Biogeographical distribution and ecological ranges of benthic cyanobacteria in East Antarctic lakes. FEMS Microbiology Ecology 57: 272-289. doi: 10.1111/j.1574-6941.2006.00110.x
- Taton, A., Grubisic, S., Brambilla, E., De Wit, R., and Wilmotte, A. 2003. Cyanobacterial diversity in natural and artificial microbial mats of Lake Fryxell (McMurdo Dry Valleys, Antarctica): a morphological and molecular approach. Applied and Environmental Microbiology 69(9): 5157-5169. doi: 10.1128/AEM.69.9.5157–5169.2003
- Thompson, D.W.J., Solomon, S., Kushner, P.J., England, M.H., Grise, K.M., and Karoly, D.J. 2011. Signatures of the Antarctic ozone hole in Southern Hemisphere surface climate change. Nature Geoscience 4: 741-749.
- Tin, T., Fleming, Z.L., Hughes, K.A., Ainley, D.G., Convey, P., Moreno, C.A., Pfeiffer, S., Scott, J., and Snapes, I. 2009. Impacts of local human activities on the Antarctic environment. Antarctic Science 21(1): 3-33. doi: 10.1017/S0954102009001722
- Tockner, K., Malard, F., and Ward, J.V. 2000. An extension of the flood pulse concept. Hydrological Processes 14: 2861-2883.
- Treonis, A.M., Wall, D.H. and Virginia, R.A. 1999. Invertebrate biodiversity in Antarctic dry valley soils and sediments. Ecosystems 2(6): 482-492. doi: 10.1007/s100219900096
- Turner, J., Arthern, R., Bromwich, D., Marshall, G., Worby, T., Bockheim, J., Di Prisco, G., Verde, C., Convey, P., Roscoe, H., Jones, A., Vaughan, D., Woodworth, P., Scambos, T., Cook, A., Lenton, A., Comiso, J., Gugliemin, M., Summerhayes, C., Meredith, M., Naveira-

- Garabato, A., Chown, S., Stevens, M., Adams, B., Worland, R., Hennion, F., Huiskes, A., Bergstrom, D., Hodgson, D.A., Bindschadler, R., Bargagli, R., Metzl, N., Van Der Veen, K., Monaghan, A., Speer, K., Rintoul, S., Hellmer, H., Jacobs, S., Heywood, K., Holland, D., Yamanouchi, T., Barbante, C., Bertler, N., Boutron, C., Hong, S., Mayewski, P., Fastook, J., Newsham, K., Robinson, S., Forcarda, J., Trathan, P., Smetacek, V., Gutt, J., Pörtner, H.-O., Peck, L., Gili, J.-M., Wiencke, C., Fahrback, E., Atkinson, A., Webb, D., Isla, E., Orejas, C., Rossi, S. and Shanklin, J. 2009. The instrumental period. In Turner, J., Bindschadler, R., Convey, P., Di Prisco, G., Fahrback, E., Gutt, J., Hodgson, D.A., Mayewski, P.A. and Summerhayes, C.P., Eds. Antarctic climate change and the environment. Cambridge, UK: Scientific Committee for Antarctic Research, 183–298.
- van Dongen, B.E., Schouten, S., and Sinninghe Damsté, J.S. 2002. Carbon isotope variability in monosaccharides and lipids of aquatic algae and terrestrial plants. *Marine Ecology Progress Series* 232: 83–92.
- Vannote, R.L., Minshall, G.W., Cummins, K.W., Sedell, J.R., and Cushing, C.E. 1980. The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* 37: 130-137.
- Varin, T., Lovejoy, C., Jungblut, A.D., Vincent, W.F., and Corbeil, J. 2010. Metagenomic profiling of Arctic microbial mat communities as nutrient scavenging and recycling systems. *Limnology and Oceanography* 55: 1901-1911. doi:10.4319/lo.2010.55.5.1901
- Velázquez, D., Rochera, C., Camacho, A., and Quesada, A. 2011. Temperature effects on carbon and nitrogen metabolism in some Maritime Antarctica freshwater phototrophic communities. *Polar Biology* 34: 1045-1055.
- Villeneuve V., Vincent, W.F., and Kómarek, J. 2001. Community structure and microhabitat characteristics of cyanobacterial mats in an extreme high Arctic environment: Ward Hunt Lake. *Nova Hedwigia* 123: 199–224
- Vincent, W.F. 2000. Cyanobacterial dominance in the polar regions. In Whitton, B.A. and Potts, M., Eds. *The ecology of cyanobacteria: their diversity in time and space*. Dordrecht, Netherlands: Kluwer Academic Publisher, 321-340.
- Vincent, W.F., Castenholz, R.W., Downes, M.T., and Howard-Williams, C. 1993a. Antarctic cyanobacteria - light, nutrients, and photosynthesis in the microbial mat environment. *Journal of Phycology* 29(6): 745-755. doi: 10.1111/j.0022-3646.1993.00745.x
- Vincent, W.F., Downes, M.T., Castenholz, R.W., and Howard-Williams, C. 1993b. Community structure and pigment organisation of cyanobacteria-dominated microbial mats in Antarctica. *European Journal of Phycology* 28: 213-221.
- Vincent, W.F., Gibson, J.A.E., Pienitz, R., Villeneuve, V., Broady, P.A., Hamilton, P.B., and Howard-Williams, C. 2000. Ice shelf microbial ecosystems in the high Arctic and implications for life on Snowball Earth. *Naturwissenschaften* 87(3): 137-141. doi: 10.1007/s001140050692

- Vincent, W.F., and Howard-Williams, C. 1986. Antarctic stream ecosystems: physiological ecology of a blue-green algal epilithon. *Freshwater Biology* 16: 219-233. doi: 10.1111/j.1365-2427.1986.tb00966.x
- Vincent, W.F., and Howard-Williams, C. 1989. Microbial communities in southern Victoria Land streams (Antarctica) II. The effects of low temperature. *Hydrobiologia* 172: 39-49.
- Vincent, W.F., and Howard-Williams, C. 2000. Life on Snowball Earth. *Science* 287: 2421.
- Vincent, W.F., and James, M.R. 1996. Biodiversity in extreme aquatic environments: Lakes, ponds, and streams of the Ross Sea sector, Antarctica. *Biodiversity and Conservation* 5: 1451-1471.
- Vincent, W.F., Mueller, D.R., and Bonilla S. 2004. Ecosystems on ice: the microbial ecology of Markham Ice Shelf in the high Arctic. *Cryobiology* 48: 103–112.
- Vincent, W.F., and Quesada, A. 2012. Cyanobacteria in high latitude lakes, rivers and seas. In Whitton, B.A., Ed. *Ecology of cyanobacteria II: their diversity in space and time*. Dordrecht, Netherlands: Springer Science & Business Media, 371-385.
- Virginia, R.A., Wall, D.H. 1999. How soils structure communities in the Antarctic Dry Valleys. *Bioscience* 49: 973-983.
- Vuorio, K., Meili, M. and Sarvala, J. 2006, Taxon-specific variation in the stable isotopic signatures ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of lake phytoplankton. *Freshwater Biology*, 51: 807–822. doi: 10.1111/j.1365-2427.2006.01529.x
- Vyverman, W., Verleyen, E., Sabbe, K., Vanhoutte, K., Sterken, M., Hodgson, D.A., Mann, D.G., Juggins, S., Van de Vijver, B., Jones, V., Flower, R., Roberts, D., Chepurnov, V.A., Kilroy, C., Vanormelingen, P., and de Wever, A. 2007. Historical processes constrain patterns in global diatom diversity. *Ecology* 88(8): 1924–1931.
- Vyverman, W., Verleyen, E., Wilmotte, A., Hodgson, D., Willems, A. Peeters, K. Van De Vijver, B., De Wever, A., Leliaert, F., and Sabbe, K. 2010. Evidence for widespread endemism among Antarctic micro-organisms. *Polar Science* 4: 103-113. doi: 10.1016/j.polar.2010.03.006
- Walsh, J.E. 2009. A comparison of Arctic and Antarctic climate change, present and future, *Antarctic Science* 21: 179-188. doi: 10.1017/S0954102009001874.
- Walvoord, M.A., and Striegl, R.G. 2007. Increased groundwater to stream discharge from permafrost thawing in the Yukon River basin: Potential impacts on lateral export of carbon and nitrogen. *Geophysical Research Letters* 34: L12402. doi:10.1029/2007GL030216
- Ward, J.V., and Stanford, J.A. 1983. The intermediate disturbance hypothesis: an explanation for

- biotic diversity patterns in lotic ecosystems. In Fontaine, T.D. and Bartell, S.M., Eds. Dynamics of lotic ecosystems. Ann Arbor, MI, Ann Arbor Science Publishers, 347-356.
- Ward J.V., and Stanford, J.A. 1995. The serial discontinuity concept: Extending the model to floodplain rivers. *Regulated Rivers: Research & Management* 10(2-4): 159-168. doi: 10.1002/rrr.3450100211
- Warnock, J.P., and Doran, P.T. 2013. Distribution of silicious-walled algae in Taylor Valley, Antarctica lakes. *International Journal of Geosciences* 4: 688-699. doi: 10.4236/ijg.2013.44064
- Welch, K.A., Lyons, W.B., Whisner, C., Gardner, C.B., Gooseff, M.N., McKnight, D.M., and Prisco, J.C. 2010. Spatial variations in the geochemistry of glacial meltwater streams in the Taylor Valley, Antarctica. *Antarctic Science* 22: 662-672. doi:10.1017/S0954102010000702
- Welschmeyer, N.A. 1994. Fluorometric analysis of chlorophyll a in the presence of chlorophyll b and pheopigments. *Limnology and Oceanography* 39: 1985-1992. doi:10.4319/lo.1994.39.8.1985.
- West, G.S. 1927. A treatise on the British freshwater algae: in which are included all the pigmented Protophyta hitherto found in British freshwaters. Cambridge, UK: The University Press, 534 pp.
- West, B.T., Welch, K.B., and Galecki, A.T. 2006. Linear mixed models: a practical guide using statistical software. London, UK: Chapman and Hall/CRC Press.
- West, W. and West, G.S. 1911. Freshwater algae. British Antarctic Expedition (1907-1909) Science Report. Biology 1: 263-298.
- Wharton Jr., R.A., Lyons, W.B., and Des Marais, D.J. 1993. Stable isotopic biogeochemistry of carbon and nitrogen in a perennially ice-covered Antarctic lake. *Chemical Geology* 107: 159-172. doi: 10.1016/0009-2541(93)90108-U
- Wharton Jr, R.A., Parker B.C., and Simmons Jr, G.M. 1983. Distribution, species composition and morphology of algal mats in Antarctic dry valley lakes. *Phycologia* 22(4): 355-365.
- Wharton, R.A., Vinyard, W.C., Parker, B.C., Simmons, G.M., Seaburg, K.G. 1981. Algae in cryoconite holes on Canada Glacier in southern Victoria Land, Antarctica. *Phycologia* 20: 208-211.
- Whittaker, T.E., Hall, B.L., Hendy, C.H., and Spaulding, S.A. 2008. Holocene depositional environments and surface-level changes at Lake Fryxell, Antarctica. *The Holocene* 18(5): 775-786. doi: 10.1177/0959683608091797
- Whitton, B.A., Ellwood, N.T.W., and Kawecka, B. 2009. Biology of the freshwater diatom *Didymosphenia*: a review. *Hydrobiologia* 630: 1-37.

- Wolman, M.G. 1954. A method for sampling coarse river-bed material. *Transactions of the American Geophysical Union* 35: 951-956.
- Wood, S. 2014. mgcv: Mixed GAM Computation Vehicle with GCV/AIC/REML smoothness estimation. R package version 1.8-3. Available at <http://cran.r-project.org/web/packages/mgcv/index.html>. Accessed 26 Oct 2014.
- Wyatt, K. H., Rober, A.R., Schmidt, N., and Davison, I.R. 2014. Effects on desiccation and rewetting on the release and decomposition of dissolved organic carbon from benthic microalgae. *Freshwater Biology* 59: 407-416. doi:10.1111/fwb.12273
- Zah, R., Burgherr, P., Bernasconi, S.M., and Uehlinger, U. 2001. Stable isotope analysis of macroinvertebrates and their food sources in a glacier stream. *Freshwater Biology* 46: 871–882. doi: 10.1046/j.1365-2427.2001.00720.x
- Zeglin, L.H., Dahm, C.N., Barrett, J.E., Gooseff, M.N., Fitpatrick, S.K., and Takacs-Vesbach, C.D. 2011. Bacterial community structure along moisture gradients in the parafluvial sediments of two ephemeral desert streams. *Microbial Ecology* 61: 1–14.
- Zuur, A.F., Ieno, E.N., and Elphick, C.S. 2010. A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution* 1: 3-14.
- Zuur, A.F., Ieno, E.N., and Smith, G.M. 2007. *Analysing Ecological Data*. New York, NY: Springer New York, 672 pp.
- Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., and Smith, G.M. 2009. *Mixed effects models and extensions in ecology with R*. New York, NY: Springer New York, 574 pp.

APPENDIX
THE GENUS *LUTICOLA* D.G.MANN (BACILLARIOPHYTA) FROM THE MCMURDO
SOUND REGION, ANTARCTICA, WITH THE DESCRIPTION OF FOUR NEW SPECIES

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ABSTRACT

A revision of the freshwater diatom genus *Luticola* from the McMurdo Sound Region, including the McMurdo Dry Valleys and Cape Royds, Antarctica, was made to contribute to a consistent flora for the entire Antarctic Region. Detailed light and scanning electron microscopic observations, review of pertinent literature, and examination of historical and type material lead to the identification of 12 *Luticola* species. Four new species and one new combination are proposed, including *L. bradyi* sp. nov., *L. spainiae*, sp. nov., *L. macknightiae*, sp. nov., *L. transantarctica*, sp. nov., and *L. elegans*, comb. nov. stat. nov. Several of these taxa were previously identified as part of the *L. muticopsis* (Van Heurck) D.G.Mann complex; *Navicula muticopsis* f. *evoluta* W. & G.S. West, *L. muticopsis* f. *reducta* (W. & G.S. West) Spaulding, and *N. muticopsis* f. *capitata* Carlson, or mistaken for the similar *L. mutica* (Kützinger) D.G.Mann and *L. cohnii* (Hilse) D.G.Mann. Morphological features of all new species were compared to the closest morphologically similar taxa, and their ecology and biogeography are discussed. All *Luticola* species considered here show restricted Antarctic distributions, and 8 of the 12 reported species are known only from the Antarctic continent.

INTRODUCTION

Species of the genus *Luticola* D.G.Mann in Round et al. (1990: 670) are typical for terrestrial ecosystems in the Antarctic Region (Kopalová et al. 2011, Van de Vijver et al. 2011). The genus

is characterized by uniseriate striae composed of rounded to transapically elongate areolae covered internally by perforated hymens, an isolated pore in the central area, a longitudinal canal positioned within the valve wall, and a simple filiform raphe with variable raphe endings (Round et al. 1990). A book volume for the genus was recently published by Levkov et al. (2013), which included 34 Antarctic Region taxa. A large number of new *Luticola* taxa have been described from Antarctica in recent years (Esposito et al. 2008, Kopalová et al. 2011, Van de Vijver et al. 2012, Zidarova et al. 2014), making the genus one of the most species-rich in the area. The *Luticola* species of Maritime Antarctica and the sub-Antarctic Islands have been recently revised (Van de Vijver and Mataloni 2008, Kopalová et al. 2011, Van de Vijver et al. 2011, Zidarova et al. 2014), showing that the genus *Luticola* is particularly widespread in the former region with more than 25 taxa compared to the sub-Antarctic islands where only 8 taxa were found. However, focused taxonomic work on the genus from the Antarctic continent is lacking, making a complete biogeographical analysis of the Antarctic Region not possible at present.

The pioneering paper by West and West (1911) gave the world a first look into the phycological diversity of the Antarctic continent and became the taxonomic foundation for the entire region. From collections taken from Shackleton's 1907–9 expedition, two species, one variety, and two forms of *Luticola* alone were described (West and West 1911). These taxa have since become staples in Antarctic species lists (Prescott 1979, Kellogg and Kellogg 2002), making Cape Royds an important type locality for Antarctic diatoms. Numerous investigations into the algal diversity of the McMurdo Sound Region have taken place since West and West (1911), such as Fritch (1912), Fukushima (1964), Seaburg et al. (1979), Kellogg et al. (1980), and Esposito et al. (2008). However, the illustrations and descriptions in West and West (1911) were incomplete by modern standards, resulting in a lack of consensus in species identity, and

taxonomic species drift can be observed in these subsequent publications (Van de Vijver et al. 2012). Of specific concern is the complex of taxa around *L. muticopsis* (Van Heurck 1909: 12) D.G.Mann in Round et al. (1990: 671) (i.e. Van de Vijver and Mataloni 2008), consisting of (but not limited to) *Navicula muticopsis* f. *evoluta* West & West (1911: 283), *L. muticopsis* f. *reducta* (W. & G.S. West 1911: 284) Spaulding in Spaulding et al. (1997: 410), *Navicula muticopsis* f. *capitata* Carlson (1913: 14), and *Navicula muticopsiforme* West and West (1911: 284). Furthermore, the ‘force-fitting’ of Antarctic diatoms into European taxa (Jones 1996, Tyler 1996), such as *L. mutica* (Kützinger 1844: 93) D.G.Mann in Round et al. (1990: 670), *L. cohnii* (Hilse in Rabenhorst 1860: 962) D.G.Mann in Round et al. (1990: 670), and nomenclatural hybrid formae such as *Navicula mutica* f. *cohnii* (as in Baker 1967: fig. 4o) have likely obscured ecological and biogeographical data.

The McMurdo Dry Valleys (MDVs) are adjacent to Cape Royds, and are home to the McMurdo Long-Term Ecological Research (MCMLTER) program, which has been monitoring Dry Valley streams and associated algal mat transects for over 20 years (mcmlter.org). Within this long-term research, *Luticola* species have been demonstrated to dominate Antarctic stream diatom communities, both in diversity and relative abundances (Stanish et al. 2011, 2012). *Luticola* species are also present in cryoconite holes (Stanish et al. 2013), within mosses (Kohler, unpublished data), and in ponds (Sakaeva 2014). Diatoms from the MDV region have been used to interpret sediment cores taken from lakes (Spaulding et al. 1997, Whittaker et al. 2008, Konfirst et al. 2011, Warnock and Doran 2013), indicate stream flow conditions (Stanish et al. 2011, 2012), and predict community structure as a function of climatic changes (Esposito et al. 2006). In order to avoid erroneous conclusions that could be made when comparing biogeographical and ecological work from other regions (e.g. Kopalová and Van de Vijver 2013,

Kopalová et al. 2013, 2014), a standardized Antarctic taxonomy is necessary (Jones 1996), and a reinvestigation into this flora using modern methods and literature is timely.

To promote compatibility among researchers and with other localities in the Antarctic Region, we analyzed samples for the genus *Luticola* taken by the MCMLTER program, which are stored at the Institute of Arctic and Alpine Research (INSTAAR) herbarium at the University of Colorado at Boulder, USA. Additionally, we resampled the lakes of Cape Royds over a century after West and West (1911) in order to evaluate their taxonomic designations, and compare this flora with the original material sampled by Shackelton's expedition stored at the British National History Museum in London, UK. All recovered species from the genus *Luticola* were compared using the most current literature, and are discussed based on detailed light and scanning electron microscopy observations. We here describe four new *Luticola* species, create one new combination, update synonyms to the most current accepted taxonomic unit, and compare all observed McMurdo Sound species with *Luticola* from the other parts of Antarctic Region (the sub- and Maritime Antarctic islands).

MATERIALS AND METHODS

Site description

The McMurdo Dry Valleys (76° 30'–78° 30' S, 160°–164° E), are the largest ice-free area in Antarctica (~4800 km²) located along the coast of McMurdo Sound in South Victoria Land (Figure 1). Here, the terrain consists mostly of unconsolidated alluvium, but streams, ponds, and seepage areas are present in summer, hosting cyanobacterial mats and mosses (McKnight et al. 1999, Ball and Virginia 2014). The ephemeral stream networks drain into perennially ice-covered lakes on the valley floors (McKnight et al. 1999). Cape Royds is a coastal area (77° 32–

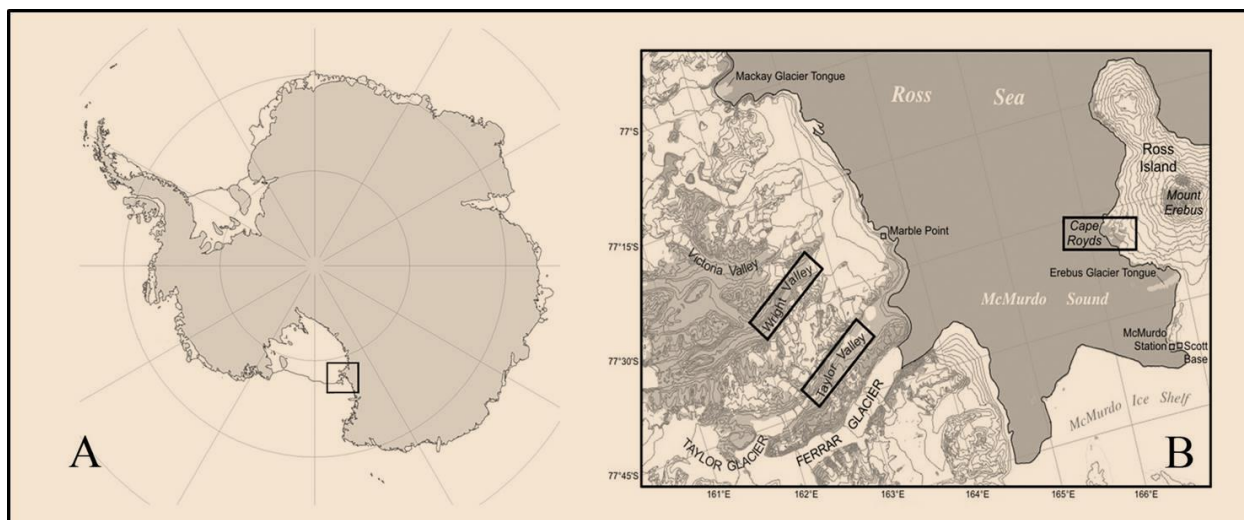


Figure 1. Map of Antarctica with detail of the McMurdo Sound region (A) along with the locations Wright Valley, Taylor Valley and Cape Royds (B). Image adapted from the US Geological Survey.

33' S, 166° 8–11' E) below the Mount Erebus volcano on the west side of Ross Island and across the McMurdo Sound from the MDVs (Figure 1). It is most famous for being the location of Shackleton's hut, which sits on the opposite side of Pony Lake from an Adélie penguin rookery. Cape Royds consists of volcanic, unconsolidated alluvium, and contains many permanently ice-covered lakes which thaw around the margins, creating “moat” areas and exposing microbial mats below.

Sample collection and analyses

In the MDVs, algal mat and moss samples are monitored along transects as part of the MCMLTER, and have been sampled annually since 1993–94 using a brass cork borer in early to mid-January. Dry Valley cryoconite holes were opportunistically sampled in January 2014 by scooping organic material with a metal spoon. At Cape Royds, lakes, seeps, and small ponds were sampled in January 2013 and 2014 with forceps to resample historical sites in West and

West (1911). All samples were put in 20 mL microcentrifuge vials or Nalgene® bottles, labeled with GPS coordinates, preserved in ~5% formalin (final concentration), and shipped to the University of Colorado. To verify identifications, we obtained the slides from West & West (1911) stored at The Natural History Museum, London (UK), to analyze the original material. All samples used for this study are listed in Table 1, along with sample locations, sample accession numbers, and dates. Samples collected during the 2011–12, 2012–13, and 2013–14 summers with confirmed specimens are listed as accession numbers from the INSTAAR herbarium, and are available online using the Antarctic Freshwater Diatoms Website: <http://huey.colorado.edu/diatoms/about/index.php>. An exception to this is for *Luticola bradyi*, which due to its extreme rarity, but consistent identification, we included records from the last 20 years.

Algal-mat samples were digested using heat and hydrogen peroxide (H₂O₂), rinsed several times with distilled water, dried onto cover slips, and permanently mounted on glass microscope slides with Zrax® mounting medium (W.P. Dailey, University of Pennsylvania). Light microscope analyses were performed using an Olympus Vanox microscope (Japan) at 1250× magnification. Scanning electron microscope (SEM) images were made after being air-dried onto aluminum stubs, and sputter-coated with 50 nm of Au (or 20 nm of Au-Pd in London). Some samples for SEM were additionally filtered through cellulose membrane filters with a 0.8 µm pore diameter prior to analysis. Material was observed at Charles University in Prague, Czech Republic (Figures 11, 29, 55–56, 74, 119–120, and 140–141), using a JEOL JSM-6380LV SEM (20 and 25 kV), the Botanic Garden Meise, Belgium (Figure 20), with a JEOL-5800LV SEM (25 kV), the National History Museum, London, UK (Figures 47 and 83), with a ZEISS ULTRA SEM (3 kV), the Nanomaterials Characterization Facility at the University of

Table 1. INSTAAR diatom collection accession numbers, sample date, name of collector, GPS coordinates, and notes for all samples used in this study.

Sample ASSN number	Sampling date	Collector	Coordinates (GPS)	Location description
INSTAAR #566-BCGB03#3	8/1/2003	D. M. McKnight	S77.62331°/E163.05767°	<i>Nostoc</i> mat sample from the margin of Bowles Creek, Taylor Valley.
INSTAAR #2657-CC9	10/1/2014	A. Mass	S77.58560°/E163.30145°	Sediment from a Commonwealth Glacier cryoconite hole, Taylor Valley.
INSTAAR #2467-11	24/1/2013	T.J. Kohler	S77.54224°/E166.14967°	Floating marginal mat from Coast Lake, Cape Royds.
INSTAAR #2477-21	24/1/2013	T.J. Kohler	S77.54115°/E166.15671°	Floating marginal mat from Clear Lake, Cape Royds.
INSTAAR #2475-19	24/1/2013	T.J. Kohler	S77.54947°/E166.15620°	Sampled from a green algae patch at the margin of Green Lake, Cape Royds.
INSTAAR #2350-O2	29/12/2012	T.J. Kohler	S77.72679°/E162.27985°	Orange cyanobacterial mat from a tributary to Lyons Creek, Taylor Valley.
INSTAAR #958-WHC11-2	10/1/2012	T.J. Kohler	S77.72520°/E162.31097°	Orange cyanobacterial mat from Wormherder Creek, Taylor Valley.
INSTAAR #2257-CSYM1	13/1/2013	T.J. Kohler	S77.61363°/E163.05227°	Yellow moss from the margin of Canada Stream, Taylor Valley.
INSTAAR #994-OV#1	25/1/2012	T.J. Kohler	S77.52402°/E161.69628°	Cyanobacterial mat from the Onyx River at Lake Vanda, Wright Valley.
INSTAAR #2669-LPS#4	7/1/2014	A. Sakaeva	S77.55017°/E161.05023°	Orange cyanobacterial mat from a Labyrinth pond, Wright Valley.
INSTAAR #2671-NRP.13.S1	26/12/2013	A. Sakaeva	S77.68438°/E162.81473°	Cyanobacterial mat from a pond south of the Nussbaum Riegel, Taylor Valley.
INSTAAR #2665-MHR.13.U	1/2/2014	A. Sakaeva	S77.83347°/E166.63353°	Benthic algae from the upper pond on the McMurdo Hut Ridge, Ross Island.
BM 34126	*12/1908 or 1/1909	J. Murray	Unknown?	Moraine, Mt. Erebus.
BM 34124	*12/1908 or 1/1909	J. Murray	Unknown?	Moraine, Mt. Erebus.
BM 34129	Unknown?	J. Murray	Unknown?	Pond, Cape Royds.

*not clear from the original West & West (1911) publication, likely collected about 3 miles from the camp, altitude from 300 to 400 feet

Colorado at Boulder, United States (Figures 90–91 and 108–109), with a JEOL JSM 7401 field emission SEM (3 kV), and at the United States Geological Survey Microbeam Laboratory, Denver, United States (Figures 150–151), with a FEI Quanta 450 FEG field emission microscope (15 kV) at a working distance of 8 mm.

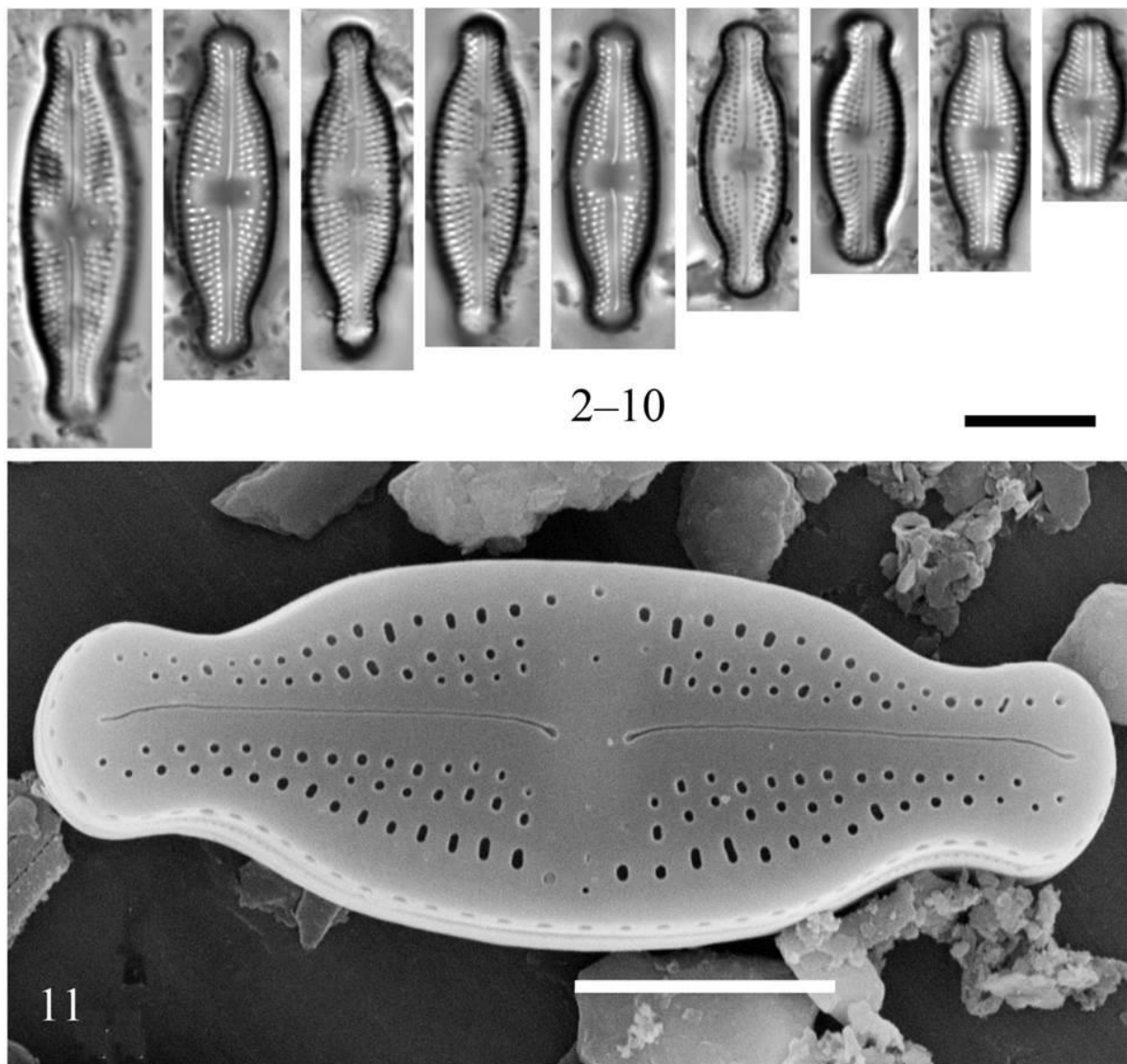
Descriptions of each taxon are given along with LM and SEM micrographs using terminology following Round et al. (1990) and Levkov et al. (2013). Resulting valve dimensions reflect the maximum and minimum measurements from a population, and stria densities reflect the range based on “n” observations. New species were compared with similar *Luticola* taxa from the Antarctic Region and globally, using Esposito et al. (2008), Van de Vijver and Mataloni (2008), Kopalová et al. (2009, 2011), Van de Vijver et al. (2011, 2012), Levkov et al. (2013), and Zidarova et al. (2014). Isotypes were sent to British Natural History Museum, London, UK, and the Botanic Garden Meise, Belgium.

RESULTS

A total of 12 different *Luticola* taxa were observed in this study, four of which could not be identified using currently available literature, even though some of these taxa were found to be the dominate species in samples. Furthermore, the geographic distributions of the observed taxa (Table 2) indicate a highly specific *Luticola* flora on the Antarctic continent.

Luticola austroatlantica Van de Vijver, Kopalová, Spaulding & Esposito in Esposito *et al.* (2008: 1383, figs. 9–27) (Figures 2–11).

Original description from Esposito et al. (2008): “Valves linear-lanceolate to elliptic-lanceolate in smaller valves, with distinctly convex margins and clearly protracted, capitate ends.



Figures 2–11. *Luticola austroatlantica* Van de Vijver, Kopalová, Spaulding & Esposito. Light (LM) and scanning electron micrographs (SEM). 2–10. Specimens from a confirmed locality, Bowles Creek, Taylor Valley, LM. 11. External valve view of specimens from a confirmed locality, Canada Stream, Taylor Valley, SEM. LM scale bar = 10 μm . SEM scale bar = 5 μm .

In smaller valves, ends only rostrate to subrostrate. Valve length 11–31 μm , valve breadth 6.4–8.7 μm . Axial area narrow and linear, becoming larger towards the central area. Central area forming a rectangular to wedge-shaped stauros bordered on each side by one or - in larger specimens - rarely by two rows of areolae. One well-isolated, rounded isolated pore present.

Raphe branches rather short and straight to weakly curved. Central raphe endings clearly deflected away from the isolated pore with slightly expanded, drop-like pores. Terminal raphe fissures short, weakly deflected and droplike expanded, terminating after the last transapical striae. Transapical striae radiate throughout, 15–17 in 10 μm , composed of 2–3 (very rarely 4) rounded to transapically elongated areolae. Outer row of areolae near the valve face margins clearly elongated. Areolae near the valve apices diverging forming a wedge-shaped hyaline area in the apices where the raphe fissures terminate. SEM: Externally, striae are not present at the valve/mantle interface. A single row of areolae is visible on the valve mantle. Distal raphe terminates in a narrow hyaline area. Isolated pore opens as a simple external pore. Internally, striae lack distinct openings and are transapically elongate. Isolated pore opening a curved and lipped slit.”

LM observations:—(Figures 2–10) Valves linear-lanceolate to elliptical-lanceolate with two convex margins. Apices distinctly capitate with constriction most pronounced on isolated pore side, becoming truncate to rostrate in smaller specimens (Figures 9–10). Valve dimensions (n=37): length 6.4–30.0 μm , width 4.4–8.2 μm . Axial area linear, slightly widening at apices and central area. An isolated pore present in the central area, halfway between the center and valve margin. Central area rectangular to bow-tie shaped, bordered by shortened striae on both sides. Raphe branches straight, deflecting away from isolated pore at both proximal and distal ends. Transapical striae radiate throughout, 16–21 in 10 μm .

SEM observations:—(Figure 11) Striae composed of 2–3 areolae, 1–2 at apices. Areolae rounded, elongated at valve margins, not extending past distal raphe endings. Isolated pore rounded. Central area bordered by a single row of three rounded areolae on both sides. Proximal raphe endings resolve into open pores, deflect away from isolated pore. Distal raphe endings

deflect away from the isolated pore, but slightly curve in the opposite direction at ends, resolving into small pores on valve face. Clear separation between valve face areolae and valve margins. A single row of rounded areolae present along entire valve mantle, not interrupted at apices.

Habitat, ecology and distribution:—*Luticola austroatlantica* is known only from Maritime and continental Antarctica. It is abundant in MDV streams, and was co-described from populations from Bowles Creek, Canada Stream, Delta Stream, and Von Guerard Stream, all in the Fryxell basin of Taylor Valley, along with the type locality on James Ross Island. Because it was historically identified as *L. muticopsis* or a variety therein (see below), its range and distribution may be broader than is currently known. Other records that match our description come from Lake Miers in the McMurdo Dry Valleys as *Navicula murrayi* by Baker (1967: fig. 4p), Deception Island (as *L. aff. muticopsis* 1, Van de Vijver and Mataloni 2008: 463, figs. 91–99), and the West Ongul Islands as *Navicula muticopsis* var. *muticopsis* by Ko-Bayashi (1965: pl. 26–27) and *Navicula muticopsis* var. *muticopsis* f. *murrayi* (W. & G.S. West) Ko-Bayashi (1963: 9–11) by Fukushima et al. (1974: pl. 2, figs. A–C).

INSTAAR herbarium:—Aiken Creek 900–903, 2224–2228; Von Guerard Stream 905–908, 911–913, 916–919, 923–926, 928; Bowles Creek 933–936, 938–940; Commonwealth Stream 945–948, 951–954; Wormherder Creek 955; Priscu Stream 960–961; Bohner Stream 963–966; McKay Creek 976, 977–978; Wharton Creek 979–980, 982; Delta Stream 983–984, 986–987, 990–992; Onyx River 994–996, 998–999, 1001; Canada Stream 1002–1005, 1010–1011, 2257; Green Creek 1018–1019, 1021–1022, 1025–1027, 2314–2318; Lawson Creek 1030–1033, 1038, 1041; Miers Stream 1047–1049; Adams Stream 1051–1057, 1064; Relict Channel 1066–1071, 1077–1081, 1084, 1087; Lyons Stream tributary 2349–2351; Picture Pond 2670; Hughes Glacier

Pond 2679; Little Sharpe (unofficial name) 2340; Many Glaciers Pond 2492; Parera Pond 2493; Nussbaum Regal Pond (unofficial name) 2671, Spaulding Pond 2494–2496.

Observations:—This diatom has been previously identified in Taylor Valley as *N. muticopsis* and *N. muticopsis* f. *evoluta* in Kellogg et al. (1980: 176, pl. 1, figs. 10–11), and was described as a new species in Esposito et al. (2008). We measured a population from Bowles Creek, INSTAAR #566, which was indicated in Esposito et al (2008) as a sample with confirmed *L. austroatlantica*. This population measured 11.8–30.0 μm in length, 5.6–8.2 μm in width, and had 16–21 striae in 10 μm (n=14). We also measured a population taken from the far inland side of Taylor Valley in a tributary to Lyons Stream, INSTAAR #2350-O2 (Table 1). This community was composed almost exclusively of *L. austroatlantica*, and we measured valve lengths from 6.4–26.6 μm and valve widths as 4.4–7.6 μm , with 18–20(24) striae in 10 μm (n=23). Since the size series described and pictured from the Dry Valleys in Esposito et al. (2008) does not represent a complete cell cycle (only lengths of 12–17 μm are reported), this species is more variable in the MDVs than the original images and description suggest.

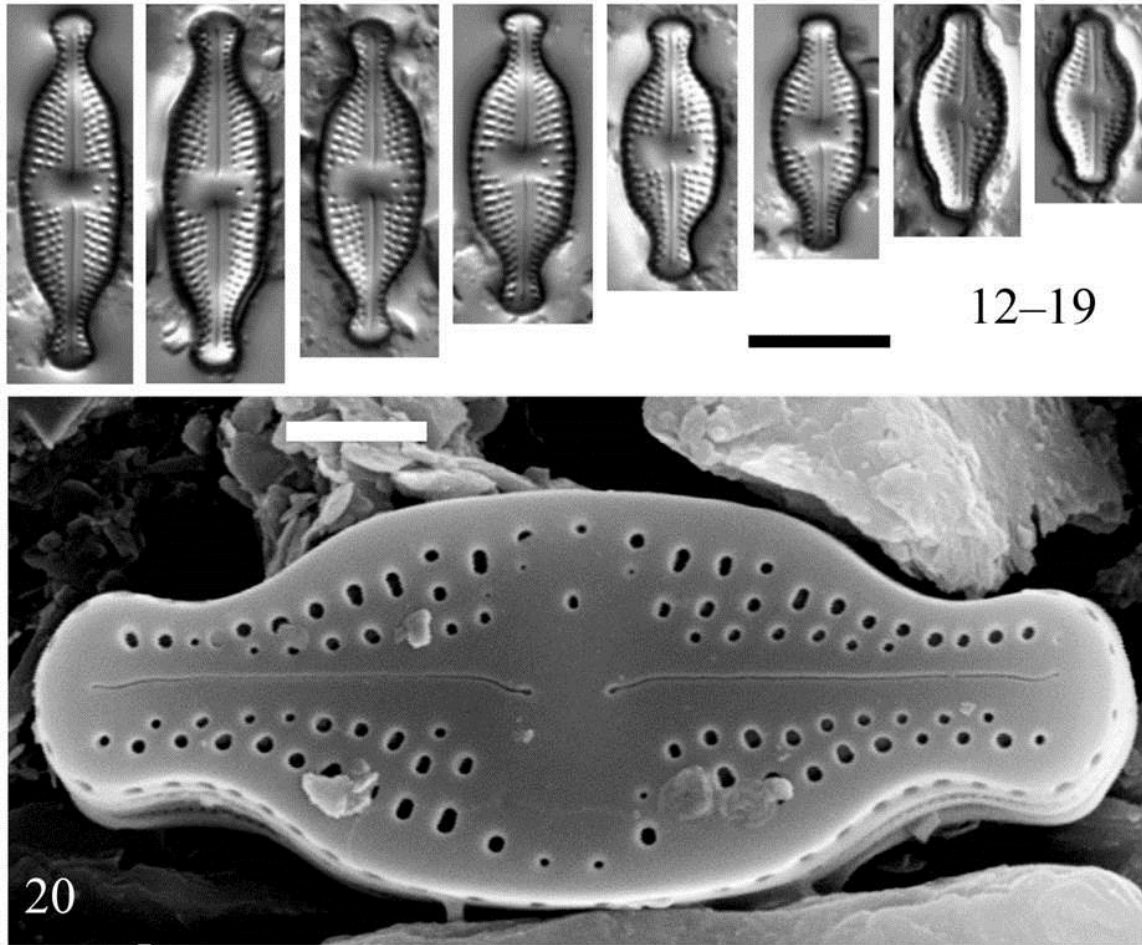
Luticola austroatlantica bears resemblance to *L. truncata* Kopalová & Van de Vijver in Kopalová et al. (2009: 118, figs. 34–50), especially at smaller and intermediate size ranges, which is present on James Ross and Livingston Islands. However, *L. truncata* is wider than *L. austroatlantica* (7.0–9.5 μm vs. 4.4–8.7 μm), has margins that are more parallel, and generally has more areolae per stria (3–5). In addition, the apices of *L. truncata* never become rounded and capitate as in *L. austroatlantica*. Among other McMurdo Sound species, *L. austroatlantica* could be confused with *L. macknightiae* Kohler & Kopalová, *sp. nov.*, especially at lower size ranges. However, *L. austroatlantica* generally has more areolae within a stria (2–3, rarely 4 vs. 1–2, rarely 3), and has more capitate apices than *L. macknightiae*. Furthermore, *L. austroatlantica* is

typically wider than *L. macknightiae* at any given length. *Luticola elegans* (West and West 1911: 285) Kohler & Kopalová *comb. nov.* is similar in valve outline to *L. austroatlantica*, though generally wider in breadth (6.4–9.5 μm vs. 4.4–8.2 μm in our population), and more areolae per stria (3–4 vs. 2–3, rarely 4). *Luticola elegans* additionally is less constricted between the capitate apices and the valve center compared to *L. austroatlantica*, and apices are generally wider. At the upper size range, *L. elegans* is more rostrate, while *L. austroatlantica* is more capitate.

Luticola dolia Spaulding & Esposito in Esposito *et al.* (2008: 1385, figs. 37–41) (Figures 12–20).

Original description from Esposito et al. (2008): “Valves broadly rounded with produced capitate ends becoming rostrate at the small end of the size range. Valve length 15–22 μm , width 5.5–8.0 μm . Axial area lanceolate. Central area rectangular or elongate-elliptical and exhibits a single row of areolae on the valve margin. A solitary isolated pore is present on one side of the valve in the central area. Central nodule is distinctly thickened. Raphe linear; both terminal raphe fissures and central raphe ends hook slightly in the opposite direction of the isolated pore. Striae are composed of punctate areolae and number 14–18 in 10 μm . Striae radiate throughout. Valve mantle is shallow.”

LM observations:—(Figures 12–19) Valves linear-elliptic with straight to convex margins, becoming slightly undulate in larger specimens (Figures 12–13). Apices highly capitate, becoming rostrate at small sizes (Figures 17–19). Valve dimensions (n=12): length 11.3–25.1 μm , width 5.4–7.7 μm . Axial area linear, opening towards central area. An isolated pore is present in the central area, located halfway between the valve center and valve margin. Central area circular to bow-tie shaped, bordered by shortened striae on both sides. Raphe branches



Figures 12–20. *Luticola dolia* Spaulding & Esposito. Light (LM) and scanning electron micrographs (SEM). 12–19. Specimens from the Onyx River, Wright Valley, as featured in Levkov et al. 2013, LM. 20. External valve view of specimens from the Onyx River, SEM. LM scale bar = 10 μ m. SEM scale bar = 2 μ m (top).

straight, deflecting away from isolated pore on distal and proximal ends. Transapical striae radiate throughout, 15–19 in 10 μ m.

SEM observations:—(Figure 20) Striae composed of 2–3 areolae, 1–2 at apices. Areolae rounded to elongated throughout, not extending past distal raphe endings on the valve face. Isolated pore rounded. Central area bordered by single row of three rounded areolae on side opposite isolated pore, 1–2 rows on isolated pore side. Proximal raphe endings deflected opposite isolated pore, with some specimens having ends that curve back slightly to the opposite

direction. Distal and proximal raphe endings terminate into linear slits or small pores on valve face. Clear separation between valve face and margins. A single row of with rounded areolae present along entire valve mantle, not interrupted at apices.

Habitat, ecology and distribution:—At present, this species is known only from the McMurdo Dry Valleys from which it was described. Even here, *Luticola dolia* is sparse throughout Taylor Valley, and rare or absent at Cape Royds (Sakaeva 2014). This species has been shown to be common in the Lake Bonney Basin of Taylor Valley, especially in Wormherder Creek (Stanish et al. 2012). In this survey, we found *L. dolia* to be abundant in the mosses of Lake Fryxell Basin streams, as well as the outlet of the Onyx River in Wright Valley.

INSTAAR herbarium:—Aiken Creek 901; Von Guerard Stream 905–908, 911–912, 916–918, 923, 925–926; Harnish Creek 928; Bowles Creek 933, 936, 939, 940; Wormherder Creek 955; Priscu Stream 960–961; Bohnert Stream 963–966; Wharton Creek 979–982; Delta Stream 986–987, 990, 992; Onyx River 994–996, 998, 1001; Canada Stream 1010, 2257; Green Creek 1019, 1022, 1027, 2316–2317; Lawson Creek 1038, 1041; Miers Stream 1048; Adams Stream 1051, 1053–1057, 1064; Relict Channel 1066, 1068, 1070, 1077–1081, 1084; Little Sharpe (unofficial name) 2340; Upland Pond 2677–2678; Spaulding Pond 2494–2496; Picture Pond 2668.

Observations:—Identified as *Navicula muticopsis* f. *capitata* in Kellogg et al. (1980: 176, pl. 1, fig.12), *L. dolia* was later described as a separate species in Esposito et al. (2008). This species is easily recognizable due to the narrow constrictions beneath the highly capitate ends. It is possible that different morphotypes are present within our concept of *L. dolia*, as differences in distal raphe endings, density of striae areolae, valve outline, and central area shape (oval vs. bow-tie) have been observed. However, assessing differences between populations of *L. dolia* is difficult both due to the rarity of this taxon, but also because of the images provided in the original

description, which are of intermediate lengths. Furthermore, these morphological differences are present within as well as among populations, making it difficult to discern if these represent intraspecific variation, or if two similar morphotypes co-occur. Our measurements in the above description were made from the same sample as pictured in Levkov et al. (2013) from the Onyx River at Lake Vanda, which had abundant *L. dolia*, and is on the other side of the Asgard Range from the type locality Delta Stream (Esposito et al. 2008), where we observed *L. dolia* to be more sparse. Additional SEM and LM images from the same population as those presented here are pictured on plate 138 of Levkov et al. (2013).

Luticola dolia is virtually unmistakable amongst other MDV *Luticola*, though it shares some similarities with *Luticola* taxa from other Antarctic localities. For example, *Luticola doliiformis* Kopalová & Van de Vijver in Kopalová et al. (2011: 49, figs. 14–28) is similar in valve outline, but differs by having broadly rounded, enlarged apices, denser striae (18–20 vs. 14–19 in 10 µm), and a wider axial area (Kopalová et al. 2011). Furthermore, *L. doliiformis* possesses smaller, more rounded areolae compared to the larger, elongated areolae in *L. dolia*. Lastly, *L. doliiformis* possesses shorter distal raphe fissures, and has an isolated pore closer to the margin than does *L. dolia* (Kopalová et al. 2011). *Luticola katkae* Van de Vijver & Zidarova in Van de Vijver et al. (2011: 143, figs. 2–15) also looks similar under LM, having similar capitate apices (Van de Vijver et al. 2011). However, *L. katkae* may have more areolae per stria (2–4 vs. 2–3), and is unmistakable under SEM due its elevated, thickened raphesternum, absent in *L. dolia*. Lastly, *L. dolia* shares several characteristics with *L. evkae* Kopalová in Kopalová et al. (2011: 51, figs. 35–50) such as similar central areas and sparse, punctate striae. However, *L. dolia* has a more elongated valve outline and less clearly convex margins than *L. evkae*. Most

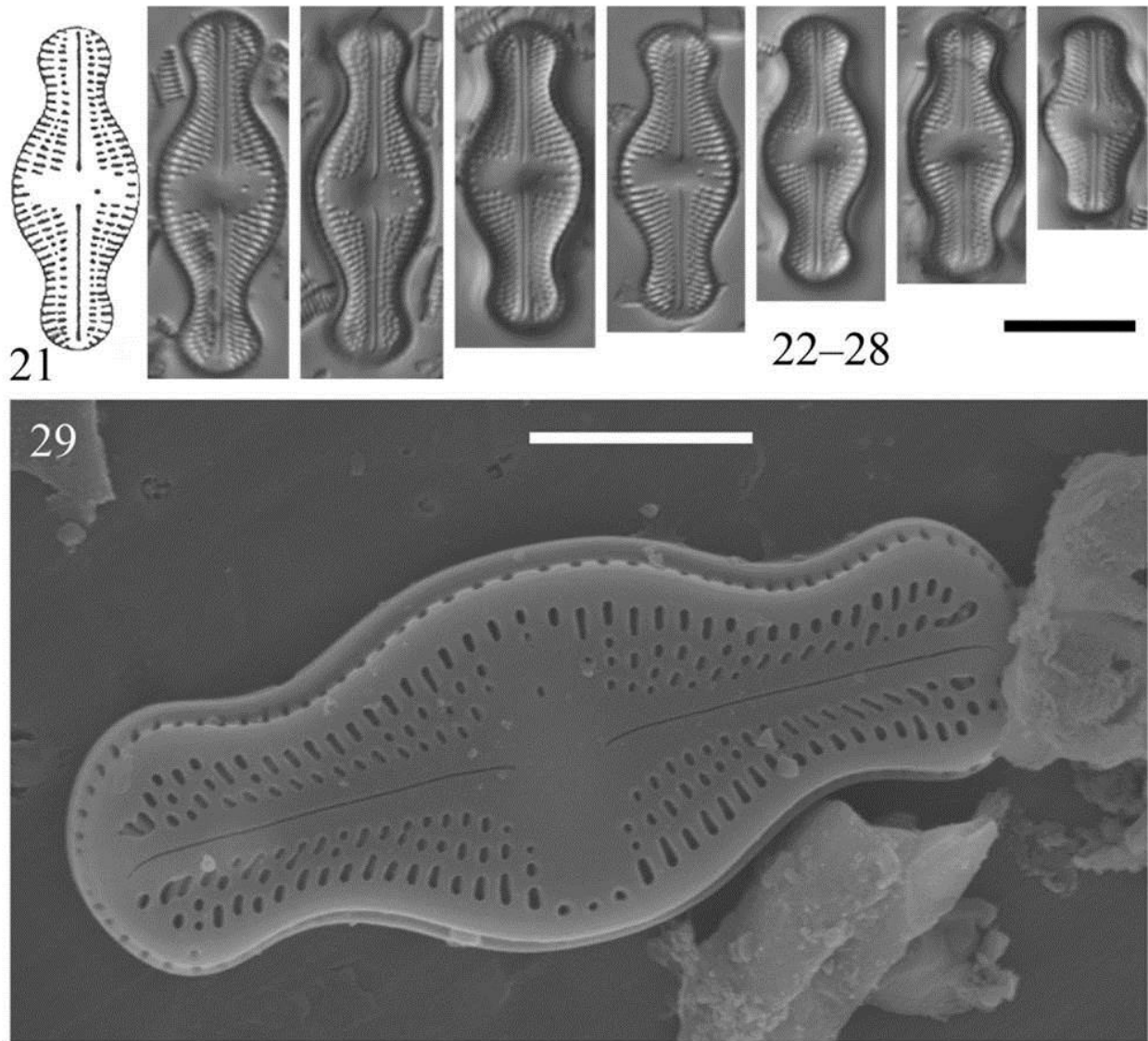
notably, *L. evkae* has broader, more capitate apices than *L. dolia*, as discussed in Kopalová et al. (2011).

Luticola gaussii (Heiden in Heiden & Kolbe 1928: 623, pl. 3, fig. 71) D.G.Mann in Round et al. (1990: 670) (Figures 21–29, Figure 21 is an original illustration from West and West (1911)).

Original description from Heiden and Kolbe (1928): “*Unterscheidet sich vom Typus durch das abgerundete, die Schalenränder nicht erreichende Mittelfeld und die etwas engere Streifung. Länge 30–31 μ , Breite 12–14 μ , Streifen 140–160 in 100 μ .*”

LM observations:—(Figures 22–28) Valves elliptical to elliptical-lanceolate with convex margins, rounded in central area. Apices broadly rounded, capitate. Valve dimensions (n=10): length 14.8–27.5 μ m, width 7.7–9.7 μ m. Axial area linear, expanding towards the central area. An isolated pore present in the central area, halfway between the valve center and valve margin. Central area rectangular, bordered by shortened striae on both sides. Raphe branches straight, deflects away from the isolated pore at both proximal and distal ends. Transapical striae radiate throughout, 19–23 in 10 μ m, with longitudinal interruptions present as illustrated by West and West (Figure 21).

SEM observations:—(Figure 29) Striae composed of 3–4 areolae, 2–3 at apices. Areolae elongated throughout, becoming broader near valve margins, sometimes extending past distal raphe endings. Isolated pore elongated. Central area bordered by a single row of three rounded areolae on both sides. Both proximal and distal raphe endings simple, slightly deflecting away from the isolated pore, resolving into slits on valve face. Clear separation between areolae and valve margins. A single row of elongated areolae present along entire valve mantle in shallow depression, interrupted at apices.



Figures 21–29. *Luticola gaussii* (Heiden) D.G. Mann. 21. Original illustration from West and West (1911: pl. 26, fig. 135). Light (LM) and scanning electron micrographs (SEM). 22–28. Specimens from Coast Lake, Cape Royds, LM. 29. External valve view of specimens from Clear Lake, Cape Royds, a confirmed West and West (1911) locality, SEM. LM scale bar = 10 μ m. SEM scale bar = 5 μ m.

Habitat, ecology and distribution:—*Luticola gaussii* was thought to be endemic to the Antarctic continent until it was recently observed from the lakes of James Ross Island, Maritime Antarctica (Kopalová et al. 2011). The earliest records from the McMurdo Sound region date from Cape Royds by West and West (1911) as *Navicula* (*Pinnularia*) *globiceps* W.Greg. (1856:

10), and noted from Green and Clear Lakes (Fig. 21). Fritch (1912) may have also found this diatom, and pictured a similar species as *Navicula globiceps* f. *amphicephala* Fritsch (1912: 54). *Luticola gaussii* is a commonly reported diatom from Dry Valley streams (Stanish et al. 2011, 2012), lakes (Baker 1967, Spaulding et al. 1997), and ponds (Sakaeva 2014), where it is generally rare in relative abundances (especially rare in *Nostoc* mats), but broad in distribution. Lastly, *L. gaussii* is a common *Luticola* species in cryoconite holes (Stanish et al. 2013).

INSTAAR herbarium:—Aiken Creek 900–902, 2224–2228; Bowles Creek 936, 938–939; Commonwealth Stream 945–948, 951–954; Priscu Stream 961; McKay Creek 975–978; Wharton Creek 979, 981–982; Delta Stream 983, 990–991; Onyx River 995–996, 999; Canada Stream 1002–1005, 1010–1011; Green Creek 1018–1019, 1021–1022, 1025–1026, 2314–2317; Miers Stream 1046, 1048–1049; Adams Stream 1052–1054, 1064; Picture Pond 2666–2668, 2670; Blue Lake 2472, 2487, 2497; Many Glaciers Pond 2492; Clear Lake 2501; Coast Lake 2502; Upland Pond 2677–2678; Spaulding Pond 2494–2496; Blue Lake 2498–2500.

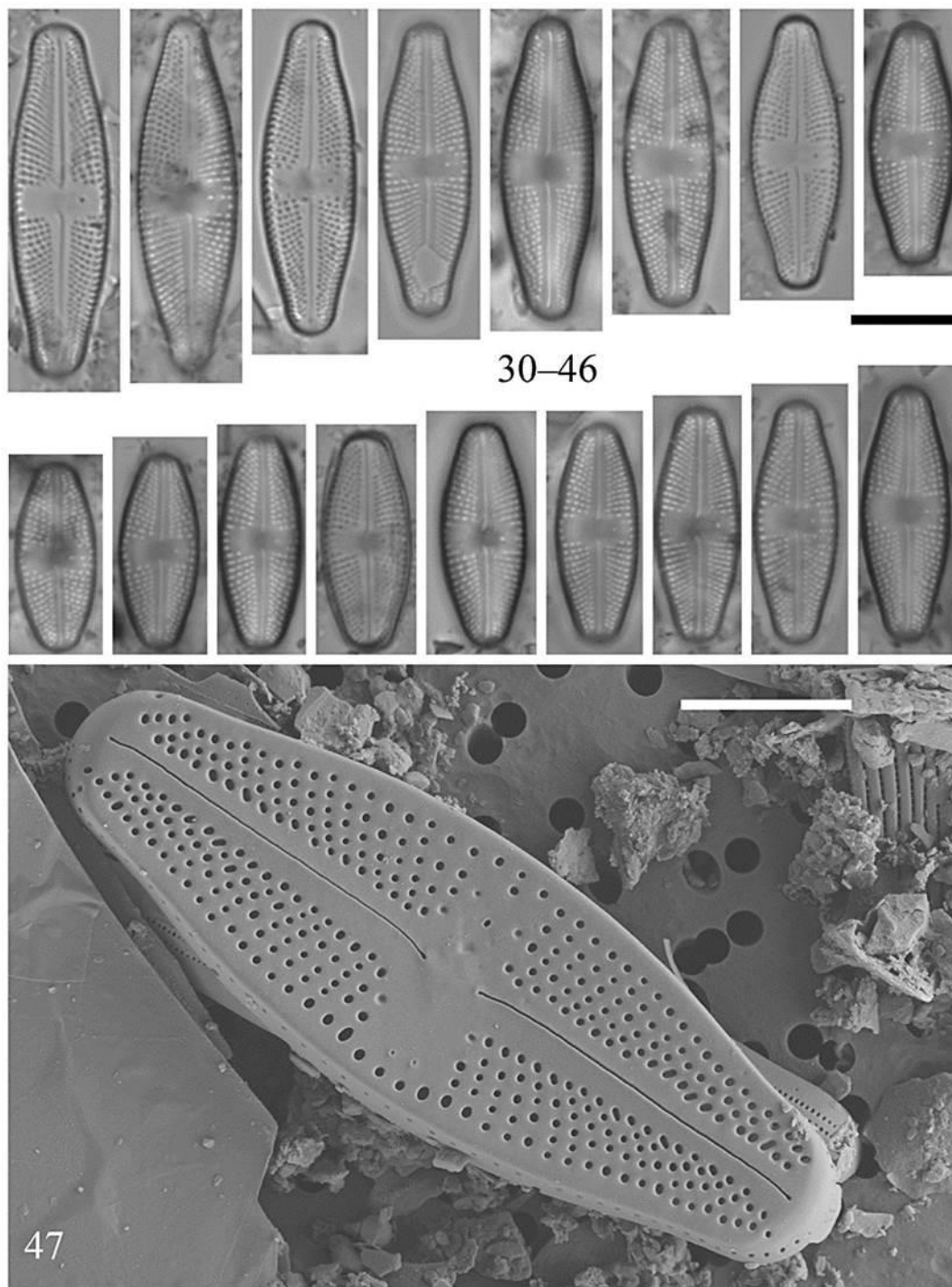
Observations:—*Luticola gaussii* was elevated to species by Hustedt (*Navicula gaussii*), and is a likely synonym with *Navicula globiceps* West and West (1911: fig. 135). *Navicula muticopsis* f. *reducta* described by West and West (1911) may also be a synonym of *L. gaussii*, due to the image in Kellogg et al. (1980: 176, pl. 1, fig.19) [but not Seaburg et al. (1979: 166, pl. 22, fig. 92)] which is likely a small valve of *L. gaussii*. In the illustration provided by West and West (1911) (as *Navicula globiceps*), it is clear that *L. gaussii* has slit-like areolae, which is confirmed by SEM (Fig. 29). Also referenced by West and West (1911) in both the text and illustration are the longitudinal interruptions in striae; two in the middle of the valve, and one at the ends, which is an important distinguishing characteristic. Our measurements agree well with Levkov et al.

(2013), who report the size of this species to be 14–34 μm length, 7.5–13.5 μm width, and having a stria density of 18–22 in 10 μm composed of 3–4 areolae.

Similar species include *L. pseudomurrayi* Van de Vijver & Tavernier in Van de Vijver et al. (2012: 164, figs. 93–110), which is often documented from East Antarctica, though not in the McMurdo Sound Region. *Luticola pseudomurrayi* has less capitate apices than *L. gaussii*, a more elongated central area, does not bear longitudinal interruptions in striae, and may have 4–5 areolae compared to 3–4 in *L. gaussii* (Van de Vijver et al. 2012). Within the McMurdo Sound Region, *L. gaussii* is most similar to *L. transantarctica* Kohler & Kopalová *sp. nov.*, which also has highly capitate apices and convex margins. However, *L. transantarctica* also does not possess the longitudinal interruptions in striae, has more elongated valve margins, and is generally narrower than *L. gaussii*. Lastly, *L. permuticopsis* Kopalová & Van de Vijver in Kopalová et al. (2011: 53, figs. 51–72), possesses a less rounded and more elongated central part of the valve, has more areolae per striae (3–6), and more angular, capitate apices.

Luticola laeta Spaulding & Esposito in Esposito et al. (2008: 1383, figs. 28–36) (Figures 30–47)

Original description from Esposito et al. (2008): “Valves linear-lanceolate with slightly rostrate ends. Valve length 22–43 μm , width 7.5–10.0 μm . Axial area narrowly lanceolate. Central area rectangular or elongate-elliptical, asymmetrical to the apical axis. A solitary isolated pore is present on the narrower side of the central area. Central nodule distinctly thickened. Raphe linear; both proximal and distal raphe ends hook slightly in the opposite direction of the isolated pore. Striae composed of punctate areolae, 16–18 in 10 μm . Striae radiate throughout, more broadly spaced in the central part of the valve. Valve mantle shallow.”



Figures 30–47. *Luticola laeta* Spaulding & Esposito. Light (LM) and scanning electron micrographs (SEM). 30–46. Specimens from a confirmed locality, Canada Stream, Taylor Valley, LM. 47. External valve view from Canada Stream, SEM. LM scale bar = 10 μm . SEM scale bar = 5 μm .

LM observations:—(Figures 30–46) Valves elliptical-lanceolate to linear-lanceolate with convex margins. Apices rounded at smaller size ranges (Figures 38–40), rostrate at upper sizes (Figures 30–36). Valve dimensions (n=13): length 17.4–35.6 μm , width 7.1–8.8 μm . Axial area linear, expanded near central area and apices. Central area rectangular to almost bow-tie shaped, bordered by shortened striae on both sides. An isolated pore present in the central area, half-way between valve center and valve margin. Raphe straight, with external distal and proximal endings deflected into the opposite direction of the isolated pore. Transapical striae radiate throughout, more broadly spaced in valve center, 18–21 in 10 μm .

SEM observation:—(Figure 47) Striae composed of 4–6 areolae, 3–4 at the apices. Areolae rounded, elongated at axial area, sometimes extending past distal raphe endings. Isolated pore rounded. Central area bordered by 1–2 rows of four rounded areolae on the isolated pore side, a single row on the opposite side. Proximal and distal raphe endings deflect away from isolated pore, terminating into small pores on valve face. Clear separation between valve face areolae and valve margins. A single row of rounded areolae present along entire valve mantle, interrupted at apices.

Habitat, ecology and distribution:—At present, this species is known only from the Antarctic continent, in the MDVs from which it was described. While it is ubiquitous throughout the Dry Valleys, albeit at low relative abundances, the greatest populations have been observed in moss samples from Canada Stream (INSTAAR #2257) and Bowles Creek (INSTAAR #566), the latter of which is the type locality (though not type-habitat) of this species. *Luticola laeta* is also a common *Luticola* species in cryoconite holes, especially on Canada Glacier (Stanish et al. 2013), though it appears to be rare in ponds and absent from Ross Island (Sakaeva 2014).

INSTAAR herbarium:—Aiken Creek 901–902, 2224–2228; Von Guerard Stream 905–908, 911–913, 916–919, 923–926; Harnish Creek 928; Bowles Creek 933, 935, 938–940; Commonwealth Stream 946, 948, 952–954; Wormherder Creek 955; Wharton Creek 982; Delta Stream 984, 986–987, 990–992; Onyx River 995; Canada Stream 1010, 2257; Green Creek 1018–1019, 1021, 1025–1026, 2315–2318; Lawson Creek 1031–1033, 1038, 1041; Miers Stream 1046–1047, 1049; Adams Stream 1051–1055, 1064; Relict Channel 1066–1071, 1077–1081, 1084, 1087.

Observations:—The smaller size range of this species has probably been identified as *L. mutica* or *L. cohnii*, which are species complexes similar to that of *L. muticopsis* (Kopalová et al. 2011), where small rounded cells have been assigned taxonomically. Described from the Northern Hemisphere, *L. mutica* is more oval-shaped and has eccentric proximal raphe endings terminating in recurved hooks (Levkov et al. 2013), a characteristic not present in any MDV *Luticola* species. *Luticola cohnii* is also a species described from Europe (as *Stauroneis cohnii* Hilse in Rabenhorst 1860). Similar to *L. laeta*, it is 19–40 μm in length, and 8.5–11.0 μm in width, but is always ovular in outline (Levkov et al. 2013). Most importantly, the external distal raphe endings in *L. cohnii* do not terminate until shortly before valve edge (Van de Vijver et al. 2011: figs. 30–31), unlike in *L. laeta*, where the external distal raphe ends terminate on the valve face.

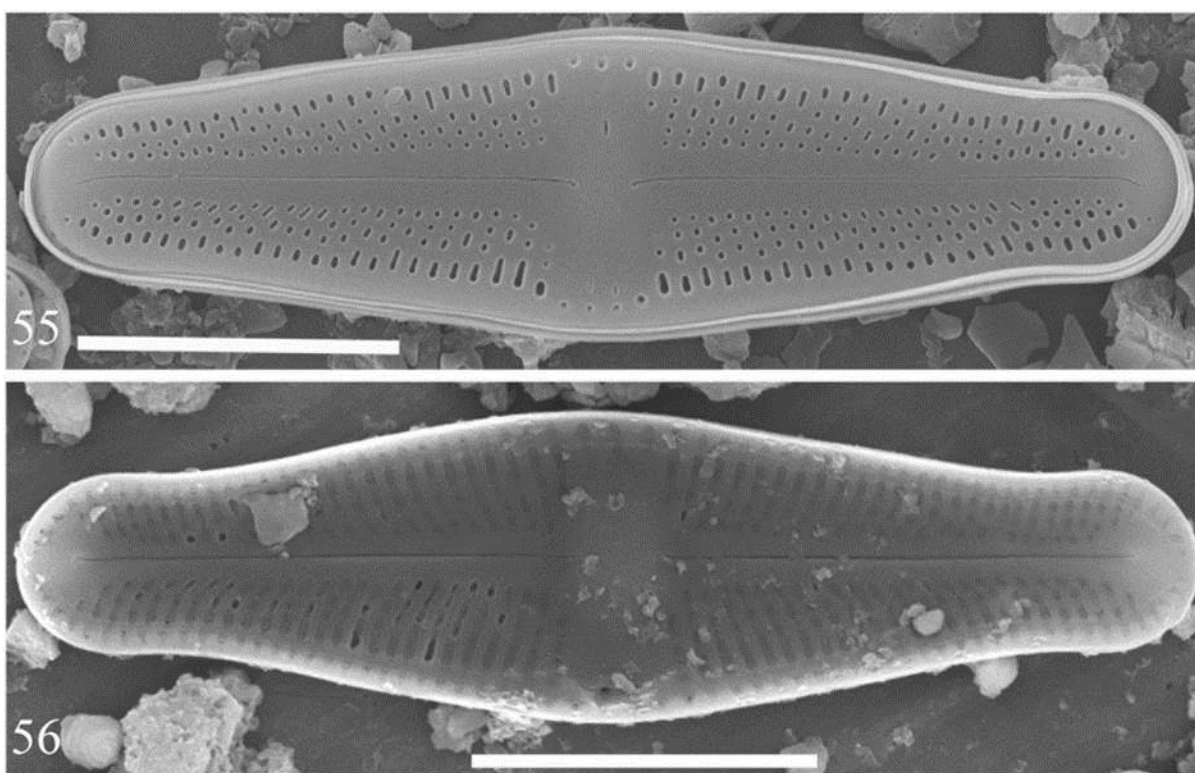
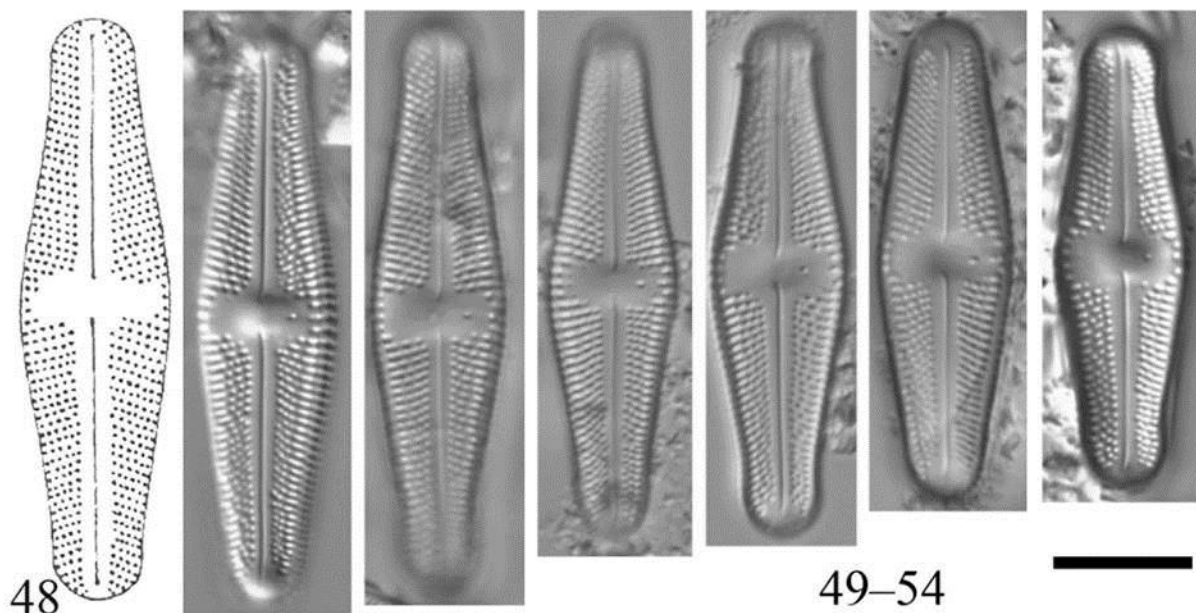
Among other *Luticola* from the Antarctic Region, *L. vermeulenii* Van de Vijver in Van de Vijver et al. (2011: 145, figs. 16–29) has a similar length range (24–50 μm), but is generally wider than *L. laeta* (9.5–14.0 μm vs. 7.5–10.0 μm) with denser striae (14–17 in 10 μm) and more elongated areolae per stria (5–7; Van de Vijver et al. 2011). *Luticola australomutica* Van de Vijver in Van de Vijver and Mataloni (2008: 458) is another similar species both in valve outline

and dimensions, with length 17–35 μm , width 6–8 μm , and stria density 16–21 in 10 μm . However, *L. austalomutica* has only 2–4 areolae per stria (compared to 4–6 in *L. laeta*), and the raphe terminates at the apices before the last row of areolae (Van de Vijver and Mataloni 2008), whereas it continues to or past the last row in *L. laeta* (Esposito et al. 2008: fig. 35). Valve sides are also generally more convex for *L. laeta*, while one side of *L. austalomutica* is flattened (Van de Vijver and Mataloni 2008).

Among MDV taxa, *L. laeta* shares similarities with *L. spainiae* Kohler & Kopalová, *sp. nov.* and *L. murrayi* (W. & G.S. West 1911: 285) D.G. Mann in Round et al. (1990: 671), especially in length and width ratios. *Luticola laeta* differs from these taxa primarily in terms of valve outline. *Luticola spainiae* has more broadly rostrate apices, and generally has fewer areolae per stria than *L. laeta* (4–5, 2–4 at apices). *Luticola murrayi* is widest in the very center of the valve, gradually tapering toward the apices, while *L. laeta* have more convex margins. Furthermore, the areolae and isolated pore in *L. laeta* are rounded, while in *L. murrayi* the outside row of areolae and isolated pore are elongated. Finally, *L. laeta* shares similarities in valve outline to *L. bradyi*, *sp. nov.*, but *L. bradyi* is both wider (10.5–12.5 μm) and longer (28.3–44.8 μm) than *L. laeta*, and has broadly rostrate to sub-capitate apices with more areolae per stria (5–7).

Luticola murrayi (W. & G.S. West 1911: 285, pl. 26, fig. 129) D.G. Mann in Round et al. (1990: 671) (Figures 48–56, Figure 48 is the original illustration by West and West (1911))

Original description from West and West (1911): “*N. parva, valvis lineari-ellipticis, diametro circiter 4-plo longioribus, polis obtusis, laevissime dilatatis, platea centrali transverse expansa, marginem utrinque paene attingente, cum puncta solitaria asymmetrica, platea axiali angusta,*



Figures 48–56. *Lenticula murrayi* (W. & G.S.West) D.G.Mann. 48. Original illustration from West and West (1911: pl. 26, fig. 129). Light (LM) and scanning electron micrographs (SEM). 49–54. LM of specimens from Green Lake, Cape Royds. 55. SEM of external valve view from population at Green Lake. 56. SEM of internal valve view from a population from a pond on the McMurdo Hut Ridge. LM scale bar = 10 μ m. SEM scale bars = 10 μ m.

striis 14 in 10 μ , punctulatis, in toto radiatis, in parte mediana 4 (circ.) utrobique multae brevioribus. Long. 45 μ ; lat, 11.5 μ .”

LM observations:—(Figures 49–54) Valves rhombic-elliptic to elliptical-lanceolate with convex margins, rapidly attenuating to broadly rounded non-protracted apices. Valve dimensions (n=52): length 28.1–40.4 μ m, width 6.8–10.2 μ m at valve center, 4.5–5.8 μ m at apices. Axial area linear, only slightly expanded near central area and apices. An isolated pore present in central area, located halfway between the valve center and valve margin. Central area rectangular to bow-tie shaped, bordered by shortened striae on both sides. Raphe branches straight, deflecting away from isolated pore at both distal and proximal ends. Transapical striae irregular, radiate throughout, 12–16 in 10 μ m, 14–18 in 10 μ m towards apices.

SEM observations:—(Figures 55–56) Externally (Figure 55), striae composed of 3–5 areolae, 2–3 at apices. Areolae elongated and slit-like throughout, becoming more rounded towards central area, extend past distal raphe endings. Isolated pore slit-shaped. Central area bordered on both sides by a single row of 3–4 rounded areolae positioned closer to valve margin than other striae. Distal raphe endings terminate on valve face on before margins, deflected away from isolated pore. Proximal raphe endings defect away from isolated pore, terminate as small pores. Clear separation between valve face and margin, with clear open area at apices around distal raphe endings. A single row of rounded areolae visible along valve mantle. Internally (Figure 56), central nodule slightly thickened. Both proximal and terminal raphe endings slightly deflected towards isolated pore. Marginal canal slightly visible. Areolae covered by hymenes. Isolated pore covered by solid silica flap.

Habitat, ecology and distribution:—*Luticola murrayi* was described from Cape Royds, Ross Island, as *Navicula murrayi* by West and West (1911). Although commonly referred to in the

literature and widely reported from a large number of Antarctic localities (Prescott 1979), this species is often confused with other *Luticola* species and reported distributions should be interpreted with caution. Illustrated specimens from the literature that match our concept of *L. murrayi* include reports from Mirny and Molodezhnaya Stations (as *Navicula muticopsis* f. *murrayi*, Fukushima 1966: fig. 1d) and the greater Ongul Islands at Lützow Holm Bay (as *Navicula globiceps* var. *elongata*, Ko-Bayashi 1963, pl. 4, fig. 2, and as *Navicula muticopsis* var. *muticopsis* f. *murrayi*, Fukushima et al. 1974: pl. 2 fig. D). This species has been commonly reported from Southern Victoria Land (as *Navicula muticopsis* f. *murrayi*, Seaburg et al. 1979: pl. 22, fig. 91) and the MDVs, though it has probably been confused with *L. laeta* (Van de Vijver et al. 2012). While more rare in the MDVs as compared to Cape Royds where it was described (Sakaeva 2014), it has been observed in Taylor Valley streams. In all populations, it is present alongside abundant *Achnanthes taylorensis* Kellogg et al. (1980: 174, pl. 1, figs. 3–4, pl. 2 figs. 1–2) and *Navicula shackletoni* W. & G.S. West (1911: 286, pl. 26, figs. 136–138).

INSTAAR herbarium:—Pony Lake 2354, 2355; Coast Lake 2467–2468; Green Lake 2473–2475, 2503; Blue Lake 2487, 2497; Picture Pond 2666–2667, 2670.

Observations:—There is a lack of consensus on the concept of *L. murrayi*, probably because the original species description, as well as for its variety, *Navicula (Pinnularia) murrayi* var. *elegans* (West and West 1911: 285, pl. 26, fig. 130), was made from the measurement of one valve. Dimensions are given as single values; length 45 µm, width 11.5 µm and 14 striae in 10 µm. No type specimen or type slide has been recovered, and only one illustration is given in the manuscript (reproduced here as Fig. 48). The illustration furthermore lacks an isolated pore, and the absence of this feature diagnostic for the genus has been a source of speculation (Ko-Bayashi 1963, Van de Vijver et al. 2012, Levkov et al. 2013). One year after its description, Fritsch

(1912) reported *Navicula murrayi* from Gap Pond, Winter Harbor, and gives a similarly vague description; length 43 µm, 10 µm width (no stria density given), and comments that it is rare. A half century later, Ko-Bayashi (1963: 13, pl. 4) reported several species from the Ongul Islands as different forms of *N. murrayi*, with the result being several new concepts that differ from the original illustration. In a classic case of species drift, one concept of *N. murrayi* by Ko-Bayashi (1963, pl. 5–7) was later reported by Hustedt (1966), Sabbe et al. (2003), and Ohtsuka et al. (2006) before finally being described as a new species, *L. pseudomurrayi*, by Van de Vijver et al. (2012) from material gathered from Lützow Holm Bay, across the continent from Ross Island.

In a recent investigation of the Cape Royds type material, Van de Vijver et al. (2012) reported that they were unable to find a single valve that matched the description of *L. murrayi* in West and West (1911). They proceeded to create a new lectotype (BM 34129) for *L. murrayi*, even though *L. murrayi* was not observed on the slide. Further, Van de Vijver et al. (2012) suggested that the true *L. murrayi* is likely a synonym with *L. laeta*, which is commonly found in the MDVs and roughly matches the illustration. However, neither Van de Vijver et al. (2012) nor the authors of this paper have observed any valves of *L. laeta* on Cape Royds or Ross Island. As a result, there is no clear evidence to support the hypothesis that the two species are conspecific.

Another concept of *L. murrayi* comes from Levkov et al. (2013), who, unlike Van de Vijver et al. (2012), report finding the true *L. murrayi* on the original West and West (1911) slides from the moraines on Mt. Erebus (BM 34124 and BM 34126), with an original note beneath two slides indicating that the species was present as evidence (Levkov et al. 2013: 539, pl. 129, figs. 29–30). On this slide were numerous capitata diatoms, along with what the authors explain to be a number of initial cells. It is these initial cells, according to Levkov et al. (2013), that most closely fit the original description and illustration, and the capitata diatoms were likely

confused with *L. muticopsis*, which are also noted to be present on the slides. Therefore, in the concept of *L. murrayi* advocated by Levkov et al. (2013), the original illustration depicts only an initial cell, and they argue that this would make sense given the lack of an isolated pore, which may be possible in initial valves. They then designated a new lectotype for *L. murrayi*, slide BM 34126.

However, the *L. muticopsis* specimens illustrated on the same plate in West and West (1911: figs. 123–124) also do not have an isolated pore (see below, Figs. 64–65) and are obviously not initial cells. The presence of an isolated pore is also discussed in the original description of *L. murrayi*, and along with the illustrated straight proximal raphe endings as noted in Van de Vijver et al. (2012), the omission of an isolated pore was most likely an oversight and not intentional. Furthermore, the initial cell presented in Levkov et al. (2013) is capitate, like the smaller-sized cells, and this is inconsistent with both the illustration and the description of *L. murrayi*. It is our opinion that the species pictured as *L. murrayi* in Levkov et al. (2013) better fit the variety “*elegans*,” which is illustrated directly beside the nominate species in the original publication (West and West 1911: 285, pl. 26, fig. 130) .

We examined the slides with the original notes (BM 34124 and BM 34126) from the London Natural History Museum, and like Levkov et al. (2013) found a capitate *Luticola* to be the dominate species on both slides, along with a few initial valves that have a similar morphology to the illustration in West and West (Fig. 57). Based on this information alone, it is reasonable to speculate that *L. murrayi* is a drawing of an initial valve and the capitate diatom is instead the real species. However, as part of our sampling of recent material on Cape Royds, we found a large population of *Luticola* that we identify as *L. murrayi* from the margin of Green Lake (INSTAAR #2475–19). These specimens are not initial valves as suggested by their

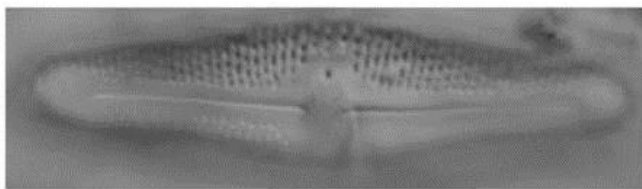
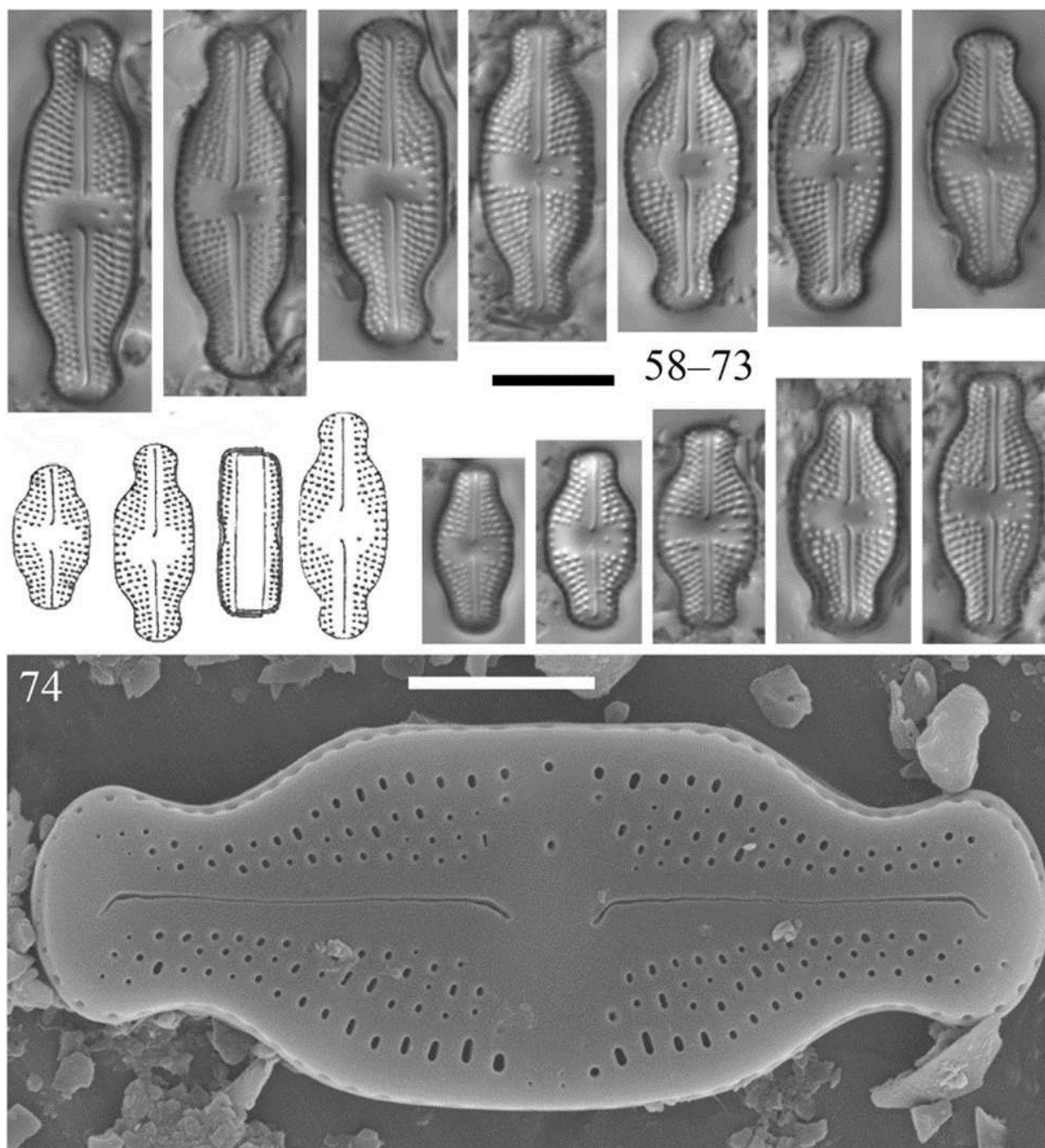


Figure 57. Initial cell from BM 34124, an original West and West (1911) slide, LM. Scale bar = 10 μ m.

57 integrity in valve outline, uniform striae, and diminution in size. At the lowest size range, this specimen overlaps with the capitate diatoms in Levkov et al. (2013), although never presenting capitate apices as part of its morphology. As a result of these observations, we suggest our concept of *L. murrayi* better fits the original description than do previous interpretations.

Luticola murrayi differs from other Antarctic species such as *L. australomutica* and *L. laeta* primarily in its valve outline, which is widest in the center and tapers to its apices into broadly rounded to sub-rostrate ends. Both the former taxa resolve into more rostrate endings, with margins of *L. laeta* being both convex, and one convex and one flattened in *L. australomutica*. *L. murrayi* furthermore has slitted outer rows of areolae, whereas areolae are generally rounded in *L. laeta*. Lastly, the distal raphe endings terminate at the last row of areolae in *L. murrayi*, unlike *L. australomutica* where the raphe terminates long before. *Luticola murrayi* further differs from the diatom it was long confused with, *L. pseudomurrayi*, by not having the broad, capitate apices present in the latter (Van de Vijver et al. 2012). *Luticola pseudomurrayi* is additionally wider than *L. murrayi* (7.5–12.0 μ m), and has more areolae per striae at apices (3–5 vs. 2–3).

Luticola muticopsis (Van Heurck 1909: 12, pl. 2, fig. 181) D.G.Mann in Round et al. (1990: 671) (Figures 58–74, Figures 65–68—first four pictures of the second row, left to right—are original illustrations by West and West (1911)).



Figures 58–74. *Luticola muticopsis* (Van Heurck) D.G. Mann. 65–68. Original illustration from West and West (1911: pl. 26, figs. 121–124). Light (LM) and scanning electron micrographs (SEM). 58–64 and 69–73. Specimens from Green Lake, Cape Royds, LM. 74. External valve view of specimens from Green Lake, Cape Royds, a confirmed locality in West and West (1911), SEM. LM scale bar = 10 µm. SEM scale bar = 5 µm.

Original Description from Van Heurck (1909): “*Valve elliptique, à extrémités brusquement et longuement rétrécies-rostrées, subparallèles, tronquées. Striae radiantes au nombre de 10 en 1 c.d.m., formées de gros granules laissant un large blanc stauronéiforme près du nodule médian et montrant un gros point isolé, unilatéral au milieu de ce pseudo-stauros. Nodules terminaux petits, semblant prolongés de chaque côté en hameçon, détail qui a été omis dans le dessin et n’est apparent que dans une autre mise au point. Longueur: 2 c.d.m., Largeur: 1 c.d.m.*”

LM observations:—Figures 58–64, 69–73. Valves linear-elliptical, with the pore-bearing valve margin straight, the opposite convex. Apices broadly capitate, becoming truncate in smaller specimens (Figures 69–70). Valve dimensions (n=10): length 13.9–31.4 μm , width 6.7–10.2 μm . Axial area present, linear, expanding toward the central area. An isolated pore present in the central area, located halfway between the valve center and valve margin. Central area rectangular to bow-tie shaped, bordered by shortened striae on both sides. Raphe straight, both proximal and distal raphe endings strongly deflecting away from the isolated pore. Transapical striae radiate throughout, 15–19 in 10 μm .

SEM observations:—(Figure 74) Striae composed of 3–5 areolae, 1–3 at apices. Areolae rounded, becoming elongated at valve margins, sometimes extending beyond distal raphe endings. Isolated pore rounded. Central area bordered by 1–2 rows of three rounded areolae on isolated pore side, one row on the opposite side. Both distal and proximal external raphe endings terminate into slits, deflecting away from isolated pore at strong, 45-degree angles on valve face. Clear separation between areolae and valve margin visible. A single row of areolae present along entire valve mantle, not interrupted at apices

Habitat, ecology and distribution:—Commonly reported from the entire Antarctic Region, such as Cape Royds on Ross Island (West and West 1911: pl. 26, figs. 121–124), the Ongul

Islands (Fukushima 1973: figs. A–E), Southern Victoria Land (Seaburg et al. 1979: pl. 22, fig. 90), James Ross (Kopalová et al. 2012: fig. 4.5x) and Deception Islands (Van de Vijver and Mataloni 2008: figs. 71–90) from the Maritime Antarctic, and the Kerguelen Islands (Levkov et al. 2013: 534, pl. 127, figs. 20–37) and Île de la Possession (Van de Vijver et al. 2002: 244, pl. 57, figs. 1–6) from the sub-Antarctic. Although widely reported, this species is probably rare in the MDVs (Sakaeva 2014).

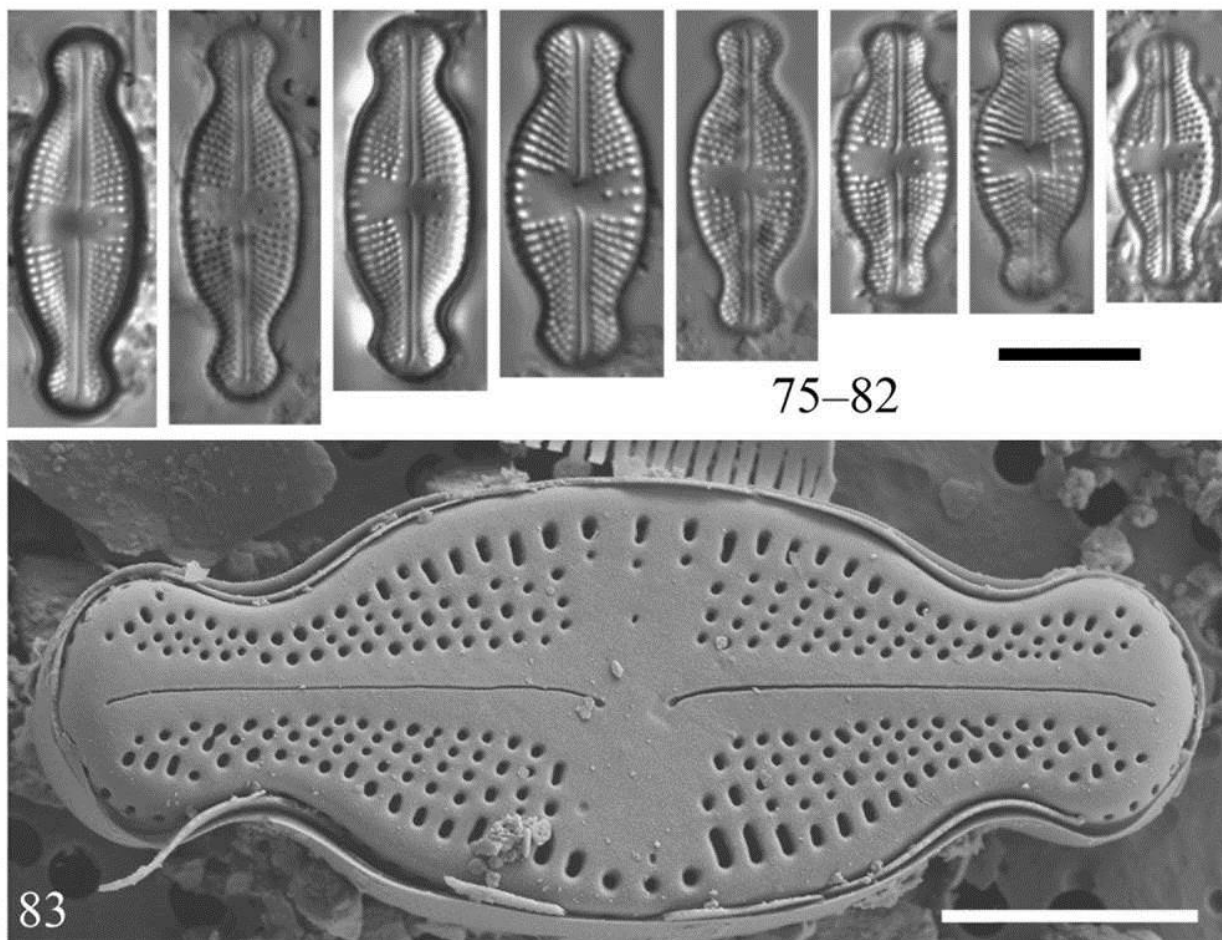
INSTAAR herbarium:—Pony Lake 2352, 2354–2355, 2662; Coast Lake 2466–2467, 2502; Green Lake 2473, 2475.

Observations:—*Luticola muticopsis* is a catch-all species complex for capitate *Luticola* species (Kopalová et al. 2011). The identity of this diatom is ambiguous due to only a single specimen present on the type slide (Van de Vijver and Mataloni 2008), and therefore has historically been a place to put all *Luticola* valves with capitate apices (Van de Vijver and Mataloni 2008) or a starting point for creating forms and varieties (i.e. West and West 1911, Ko-Bayashi 1963, 1965). After examining the Van Heurck type slide, Van de Vijver and Mataloni (2008) provided a more narrow species concept for *L. muticopsis*, and we base our concept of this diatom on their description of this valve and the Deception Island specimens included in the paper. Despite being widely reported in the MDVs (i.e. Stanish et al. 2011, 2012), *L. muticopsis* is actually observed rather infrequently in Dry Valley streams (Sakaeva 2014). This is probably due to its confusion with *L. austroatlantica*, which may have begun with the publication by Kellogg et al. 1980, where an image of what appears to be *L. austroatlantica* is labeled as *L. muticopsis*. Therefore, reports of this species prior to the description of *L. austroatlantica* in Esposito et al. (2008) should be interpreted with caution.

Luticola cognata Levkov et al. (2013) in Levkov et al. (2013: 90, pl. 130, figs. 21–38) is morphologically very similar to *L. muticopsis*. Levkov et al. (2013) indicate that *L. muticopsis* has more capitate valve apices, and that *L. cognata* is consistently wider. However, the dimensions given are 7.0–9.5 μm wide for *L. cognata* vs. 7.0–9.0 μm for *L. muticopsis*, and the differences in morphology are not easily observed in the type material as illustrated by Van de Vijver and Mataloni (2008), as well as in the Levkov et al. (2013) images of *L. muticopsis*. Therefore, it is possible that *L. cognata* is conspecific with *L. muticopsis*. *Luticola muticopsis* is also similar to *L. truncata* Kopalová and Van de Vijver in Kopalová et al. (2009: 118, figs. 34–50), especially at the lower end of the size range. However, *L. truncata* always maintains its rostrate, truncated apices, whereas *L. muticopsis* remains distinctly capitate throughout its entire size range. *Luticola muticopsis* differs from other MDV species such as *L. austroatlantica* and *L. permuticopsis* primarily by having one distinctly straight valve margin, whereas both margins in *L. permuticopsis* and *L. austroatlantica* are convex. *Luticola austroatlantica* furthermore has more elongated valve outline than *L. muticopsis*. Finally, valve apices in *L. austroatlantica* are more rounded and constricted at the neck, while *L. muticopsis* has more flattened apices that are less constricted.

Luticola permuticopsis Kopalová & Van de Vijver in Kopalová et al. (2011: 53, figs. 51–72) (Figures 75–83).

Original description from Kopalová et al. (2011): “Valves linear-lanceolate to linear-elliptic with distinctly convex margins and broadly rounded, distinctly capitate apices (Figs 51–66). Valve length 18.5–26.0 μm , valve width 7.3–9.2 μm (n=15). Axial area moderately narrow, linear (Figs 67, 68), almost not widening towards apices (Fig. 72) and central area (Fig. 71).



Figures 75–83. *Luticola permuticopsis* Kopalová & Van de Vijver. Light (LM) and scanning electron micrographs (SEM). 75–82. Specimens from Canada Stream, Taylor Valley, LM. 83. External valve view of specimens from Canada Stream, SEM. LM scale bar = 10 μm . SEM scale bar = 5 μm .

Central area forming a rectangular to wedge-shaped stauros, bordered by one series of large, rounded areolae. One solitary, almost rounded isolated pore present, usually at end of shortened stria, composed of 3 small, rounded areolae (Fig. 67) or isolated halfway between valve centre and margin (Fig. 71). External raphe branches straight with unilaterally clearly deflected, slightly expanded proximal raphe endings. Distal raphe fissures clearly elongated, deflected. Transapical striae rather strongly radiate throughout entire valve, composed of 3–6 moderately large, rounded areolae, 18–22 in 10 μm . Near central area, areolae close to margin, clearly enlarged (Figs 67,

71). Internally, areolae of valve face occluded by hymens forming a continuous strip along each stria (Fig. 69). Internal isolated pore opening consisting of almost rounded lipped slit (Fig. 70). Stauros clearly developed (Fig. 70). Internal proximal raphe endings straight, terminating on the edge of the stauros. Distal raphe endings terminating on small helictoglossae (Fig. 69).”

LM observations:—(Figures 75–82) Valves linear-elliptical with two convex margins. Apices broadly rounded, capitate throughout the size series. Valve dimensions (n=11): length 19.7–28.9 μm , width 7.6–9.4 μm . Axial area linear, widening toward central area. An isolated pore present in the central area, halfway between the valve center and valve margin. Central area bow-tie shaped and asymmetric, sometimes wider opposite isolated pore, with shortened striae present on both sides. Raphe branches straight, both proximal and distal ending deflecting away from isolated pore. Transapical striae radiate throughout, 16–22 in 10 μm .

SEM observations:—(Figure 83) Striae composed of 3–5 areolae, 2–4 at apices. Areolae rounded, elongated toward valve margin, extending to distal raphe endings. Isolated pore small, rounded. Central area bordered by 1–2 rows of three rounded to elongated areolae on isolated pore side, and a single row of four rounded areolae on opposite side. Proximal raphe endings resolve into drop-like pores, deflect away from isolated pore. Distal raphe endings resolve into smaller, slit-like pores on valve face. Clear separation between valve face areolae and valve margins. A single row of rounded areolae is present along valve margin.

Habitat, ecology and distribution:—*Luticola permuticopsis* was described recently from the lakes of James Ross Island, Maritime Antarctica (Kopalová et al. 2011), and until now has not been documented from elsewhere. This diatom occurs throughout the MDVs, but has been identified as *Navicula muticopsis* f. *capitata*. Therefore, we can confirm its distribution as

widespread throughout the Wright, Taylor, and Miers Valleys from the McMurdo Sound Region, though rare or absent on Cape Royds (Sakaeva 2014).

INSTAAR herbarium:—Aiken Creek 900–902, 2224–2228; Von Guerard Stream 905–908, 911–913, 916–919, 923–926; Harnish Creek 928; Bowles Creek 933–935, 938–940; Commonwealth Stream 945–948, 951, 954; Priscu Stream 960–961; Bohner Stream 963–966; Wharton Creek 980, 982; Delta Stream 983–984, 986–987, 990–992; Onyx River 995–996; Canada Stream 1002, 1004, 2257; Green Creek 1018, 1021–1022, 1025–1027; Lawson Creek 1030–1031, 1038, 1041; Adams Stream 1051, 1053–1057, 1064; Relict Channel 1066–1068, 1070–1071, 1077–1081, 1084, 1087; Wales Stream 1580; Lyons Stream tributary 2349; Many Glaciers Pond 2492; Parera Pond 2493; Spaulding Pond 2494–2496; Clear Lake 2501; McMurdo Hut Ridge 2664–2665; Picture Pond 2667; Nussbaum Regal Pond (unofficial name) 2671; Upland Pond 2678.

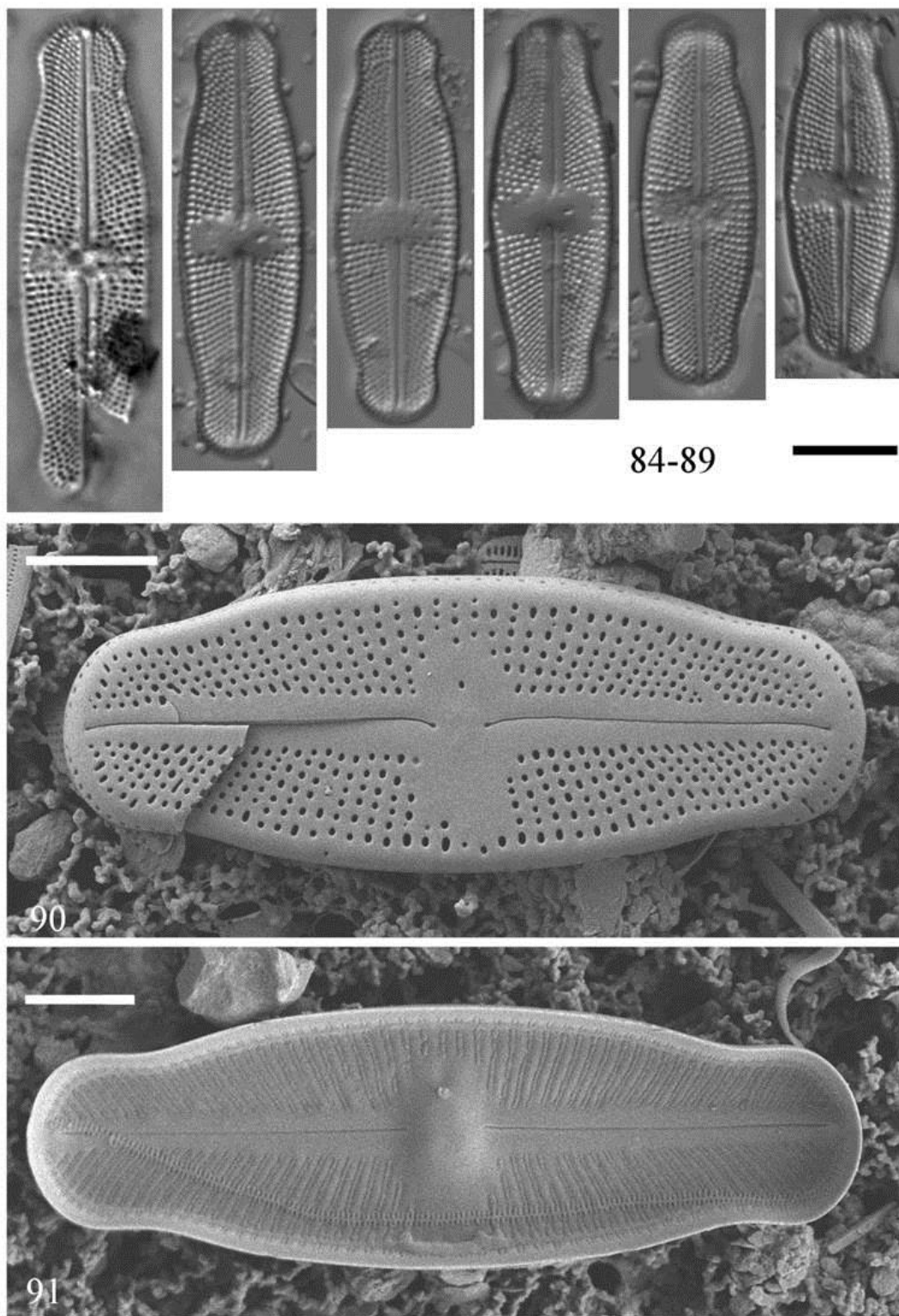
Observations:—The MCMLTER has historically identified this diatom as *N. muticopsis* f. *capitata* (Esposito et al. 2008, Stanish et al. 2011, 2012). Peragallo (1921: 17, pl. 1, fig. 40) described what is perhaps a similar species, *Navicula muticopsis* var. *capitata*, though the type material of both taxa is wanting (as discussed in Kopalová et al. 2011), and as a result the identities of these species are not verifiable. Levkov et al. (2013) only briefly mention *N. muticopsis* f. *capitata* and *N. muticopsis* var. *capitata* at the end of their book volume as probably also belonging to the genus *Luticola*, without descriptions or images. Since the existing description of *L. permuticopsis* fits our McMurdo populations well, we suggest that this taxon name be used rather than the former two, and further suggest that the range of *L. permuticopsis* from the Maritime Antarctic extends to the Antarctic continent. In the case that one of the former

names should be demonstrated to be conspecific with *L. permuticopsis*, then the name should be replaced by the first published, accepted one.

Luticola permuticopsis is most similar to *L. muticopsis* in valve outline, but *L. muticopsis* has one straight and one convex margin. This is in contrast to *L. permuticopsis*, which always has two convex margins and is generally narrower than *L. muticopsis*. The apices in *L. muticopsis* are always flattened and more rostrate, contrary to *L. permuticopsis*, which are more rounded (Kopalová et al. 2011). Furthermore, striae in *L. permuticopsis* can be composed of 3–6 areolae, whereas only 3–5 have been observed for *L. muticopsis*. Finally, the proximal and distal raphe endings in *L. permuticopsis* are weakly deflected and terminate into small pores, whereas raphe endings are deflected at strong 45-degree angles in *L. muticopsis* and resolve into slits. *Luticola permuticopsis* is also similar in morphology to *L. austroatlantica*, although *L. austroatlantica* is more narrow (4.4–8.7 vs. 7.3–9.2) and has fewer areolae per stria (2–3 vs. 3–6) (Esposito et al. 2008). Apices in *L. permuticopsis* are typically broader than in *L. austroatlantica*, and margins in *L. austroatlantica* are generally more elongated. *Luticola gaussii* also resembles *L. permuticopsis*, with both having broadly rounded apices with convex margins. However, the body of *L. gaussii* is typically more rounded than in *L. permuticopsis*, which has a more elongated mid-section. Furthermore, *L. gaussii* has striae that are only comprised of up to 3–4 areolae, whereas *L. permuticopsis* has 3–6. Lastly, a deep depression is visible around the margin of *L. gaussii* that is not present in *L. permuticopsis*.

***Luticola bradyi* Kohler, sp. nov. (Figures 84–91)**

LM observations (Figures 84–89): Valves elliptical to elliptical-lanceolate with convex margins. Apices broadly rounded, rostrate to sub-capitate. Valve dimensions (n=16): length



Figures 84–91. *Luticola bradyi* Kohler *sp. nov.* Light (LM) and scanning electron micrographs (SEM). 84–89. Specimens from Commonwealth Glacier, Taylor Valley, the type population, LM. 90. External valve view, type population, SEM. 91. Internal valve view, type population, SEM. LM scale bar = 10 μm . SEM scale bars = 5 μm .

28.3–44.8 μm , width 10.5–12.5 μm . Axial area linear, slightly widening towards the valve center. An isolated pore present in the central area, located halfway between the valve center and valve margin. Central area asymmetric, varying from elliptic to an acute-angled sub-fascia, bordered by shortened striae on both sides, wider opposite the isolated pore. Raphe branches straight, deflected away from the isolated pore at both proximal and distal ends. Transapical striae radiate throughout, more widely spaced in the central portion of the valve, 16–18 in 10 μm . **SEM observations (Figures 90–91):** Externally, (Figure 90), striae composed of 5–7 areolae, 2–4 areolae at apices. Areolae rounded, slightly elongated along the axial and marginal areas and near poles, not extending past distal raphe endings. Isolated pore rounded, slightly elongated, Central area bordered by irregular, shortened striae comprised of 3–5 rows of five rounded areolae on isolated pore side, 1–2 rows on opposite side. Proximal raphe endings deflected opposite the isolated pore, resolving into small drop-like pores. Distal raphe endings slightly deflected opposite isolated pore, terminating into small pores or fissures on the valve face. Clear separation between valve face and margins with rounded mantle areolae interrupted at apices. A single row of rounded areolae present along entire valve mantle, interrupted at apices. Internally (Figure 91), central nodule thickened. Both, proximal and terminal raphe endings straight. Distal raphe ends terminating onto very small helictoglossae. Marginal canal visible, interrupted at apices. Areolae covered by hymens, forming continuous strip along striae. Isolated pore opening covered by solid silica flap.

Type:—ANTARCTICA. McMurdo Dry Valleys: Taylor Valley, Commonwealth Glacier, cryconite hole, Sample CC-9, *A. Mass*, 10 January 2014 (holotype INSTAAR! #2657, illustrated in Fig. 88, isotypes BM! 101776, BR! 4405).

Etymology:—This species is named for Brady Kohler (Cheney, Kansas, USA), brother and best friend of the first author.

Habitat, ecology and distribution:—*Luticola bradyi* has at present only been observed from the McMurdo Sound Region, Antarctic continent. A large population of *L. bradyi* was observed during a survey of the Commonwealth Glacier cryoconite holes collected during the austral summer 2013–14. This population was found among other common cryoconite species (Stanish et al. 2013) such as *Muelleria supra* Spaulding & Esposito in Esposito et al. (2008: 1384, figs. 42–49), *M. cryoconicola* Stanish & Spaulding in Van de Vijver et al. (2010: 26, figs. 27–35), *Humidophila spp.* Lowe et al. (2014: 357), and *L. gaussii* (Levkov et al. 2013: 117, pl. 127, figs. 1–19). Aside from this population, single valves have been recovered from Cape Royds, the Onyx River in Wright Valley, and streams in the Fryxell Basin, Taylor Valley.

INSTAAR herbarium:—Lake Fryxell 390; Canada Stream 436, 527, 618, 666–667, 670, 676, 683, 689, 691, 693–694, 696–697; Green Creek 512; Relict Channel 638, 640, 739, 751, 757; Von Guerard Stream 440–441; Commonwealth Stream 888; Coast Lake 2467; Commonwealth Glacier 2657.

Observations:—Previously referred to as *L. cohnii* var. #1 (Esposito et al. 2008: 1381), this taxon was thought to be an initial cell of an unknown diatom due to its large size and scarcity. However, since a large population was found in a cryoconite hole on the Commonwealth Glacier, it is possible that this species is not rare, and is instead occasionally transported from the glaciers into streams. In valve dimensions and outline, *L. bradyi* most resembles *L. wulffii* (Peterson 1924: 312, fig. 2) Levkov et al. (2013: 259, pl. 126, figs. 19–29) which is an arctic species reported from Canada and Russia. However, *L. wulffii* has a very narrow rectangular to bow-tie shaped central area, while the central area in *L. bradyi* is broadly rectangular or elliptic.

The shortened striae in *L. wulffii* are composed of 1–2(3) areolae (Levkov et al. 2013), while the shortened striae in *L. bradyi* may number 3–5 on the side of the isolated pore. Striae in *L. bradyi* terminate more irregularly in the axial area than *L. wulffii*, which exhibits straight striae. Lastly, apices in *L. bradyi* are subcapitate at the largest sizes and become rostrate as valves become smaller. Apices in *L. wulffii* remain subcapitate, constricted where the apices meet the body, throughout the size range as illustrated in Levkov et al. (2013). These differences, along with opposite polar distributions, are sufficient to separate these two species from each other. *Luticola magellanica* (Frenguelli 1924: 95, pl. 6, fig. 37) Levkov et al. (2013: 153, pl. 41, figs. 12–19), described from Tierra del Fuego, is also similar in outline, but has denser striae (14–18 in 10 μm) and never develops constrictions at the apices; the apices are rounded.

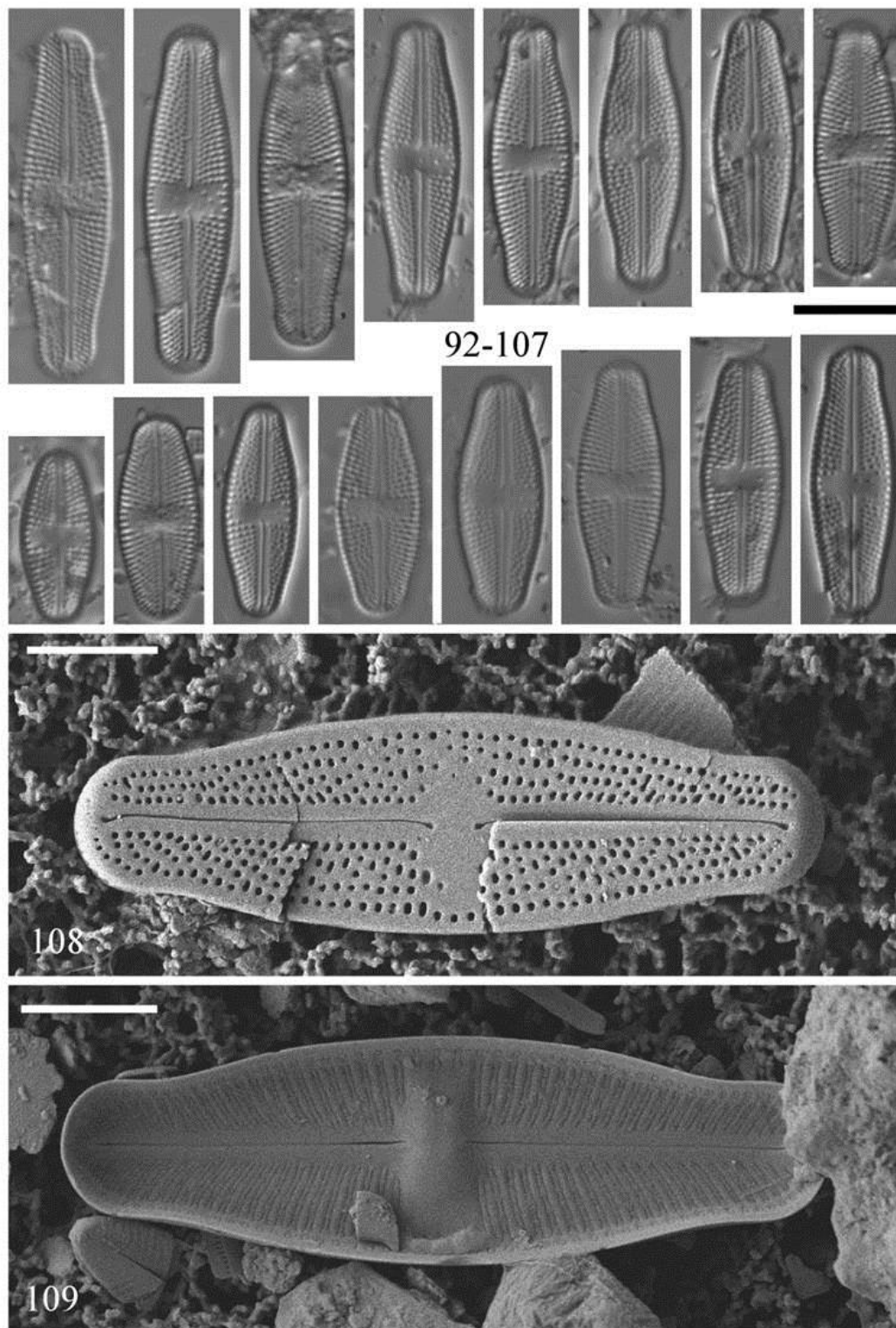
In Antarctica, *L. vermeulenii* is similar in valve length and width range (24–50 μm , 9.5–14.0 μm), though slightly longer than our observed population of *L. bradyi*. *Luticola vermeulenii* also has denser striae (14–17 in 10 μm vs. 17–21 in 10 μm) and differs in valve outline, never forming constrictions at the apices like the subcapitate endings in *L. bradyi* at the upper size ranges. Another species that bears some resemblance based on valve outline and valve length, is *L. vandevijveri* Kopalová, Zidarova & Levkov in Levkov et al. (2013: 247, pl. 10, figs. 1–24), described from James Ross Island. The latter is however narrower (maximal width 9.0 μm) giving it a more slender outlook, and has a lower number of areolae per stria. In the McMurdo Sound Region, *L. bradyi* is most similar to *L. spainiae* and *L. laeta*, which are also common cryoconite species (Stanish et al. 2013). However, most differences between these two species are found with respect to valve size. *Luticola bradyi* is generally much larger in length and width compared to *L. spainiae* and *L. laeta*, as well as most other *Luticola*. Lastly, the apices of *L. bradyi* are broadly rostrate, becoming subcapitate at larger size ranges. This differs from the

apices of *L. laeta*, which are always more narrow and never become constricted where they meet the central area.

***Luticola spainiae* Kohler & Kopalová, *sp. nov.* (Figures 92–109)**

LM observations (Figures 92–107): Valves elliptical to elliptical-lanceolate with two convex margins. Apices rounded at the lower size range (Figures 100–101), broadly rostrate to subcapitate at upper sizes (Figures 92–99). Valve dimensions (n=22): length 12.1–33.6 μm , width 6.4–8.7 μm . Axial area linear, slightly widening towards the central area. An isolated pore present in the central area, located halfway between the valve center and valve margin. Central area bow-tie shaped to almost rectangular, bordered on both sides by shortened striae. Raphe branches straight, deflected away from the isolated pore at both proximal and distal ends. Transapical striae irregular, radiate throughout entire valve, 19–22 in 10 μm .

SEM observations (Figures 108–109): Externally (Figure 108), striae composed of 4–5 areolae, 2–4 at apices. Areolae rounded, becoming slightly elongated near axial area and at poles, extending beyond distal raphe endings. Isolated pore small, rounded. Central area bordered by 2–3 rows of four rounded areolae on isolated pore side, and a single row of four on opposite side. Proximal and distal raphe endings open drop-like pores and deflect away from isolated pore. Distal raphe endings terminate on the valve face. Clear separation between valve face and margins. Internally (Figure 109), central nodule thickened. Both proximal and distal raphe endings straight. Distal raphe endings terminating onto very small helictoglossae. Marginal canal visible, interrupted at apices. Areolae covered by hymenes, forming a continuous strip along each stria. Isolated pore opening covered by solid silica flap.



Figures 92–109. *Luticola spainiae* Kohler & Kopalová, *sp. nov.* Light (LM) and scanning electron micrographs (SEM). 92–107. Specimens from Commonwealth Glacier, Taylor Valley, the type population, LM. 108. External valve view, type population, SEM. 109. Internal valve view, type population, SEM. LM scale bar = 10 μ m. SEM scale bars = 5 μ m.

Type:—ANTARCTICA. McMurdo Dry Valleys: Fryxell Lake Basin, Commonwealth Glacier, cryconite hole, Sample CC-9, A. Mass, 10 January 2014 (holotype INSTAAR! #2657, illustrated in Fig. 95, isotypes BM! 101777, BR! 4406).

Etymology:—*Luticola spainiae* is named in honor of our friend and colleague, Rae Spain, whose years as the Lake Hoare camp manager have facilitated decades of research in the McMurdo Dry Valleys in addition to providing visitors a home away from home.

Habitat, ecology and distribution:—*Luticola spainiae* is at present known only from the Commonwealth Glacier cryoconite holes, Taylor Valley, Antarctic continent. Found alongside *L. bradyi* as well as other common cryoconite species, such as *Muelleria supra*, *M. cryoconicola*, *M. peraustralis* (W. & G.S. West 1911: 284) Spaulding & Stoermer in Spaulding and Stoermer (1997), *Humidophila* spp., and *L. gaussii* (Stanish et al. 2013). Due to similarities with *L. laeta*, *L. mutica*, and *L. bradyi*, this species may be under-reported from the McMurdo Sound Region.

INSTAAR herbarium:—Commonwealth Glacier 2657

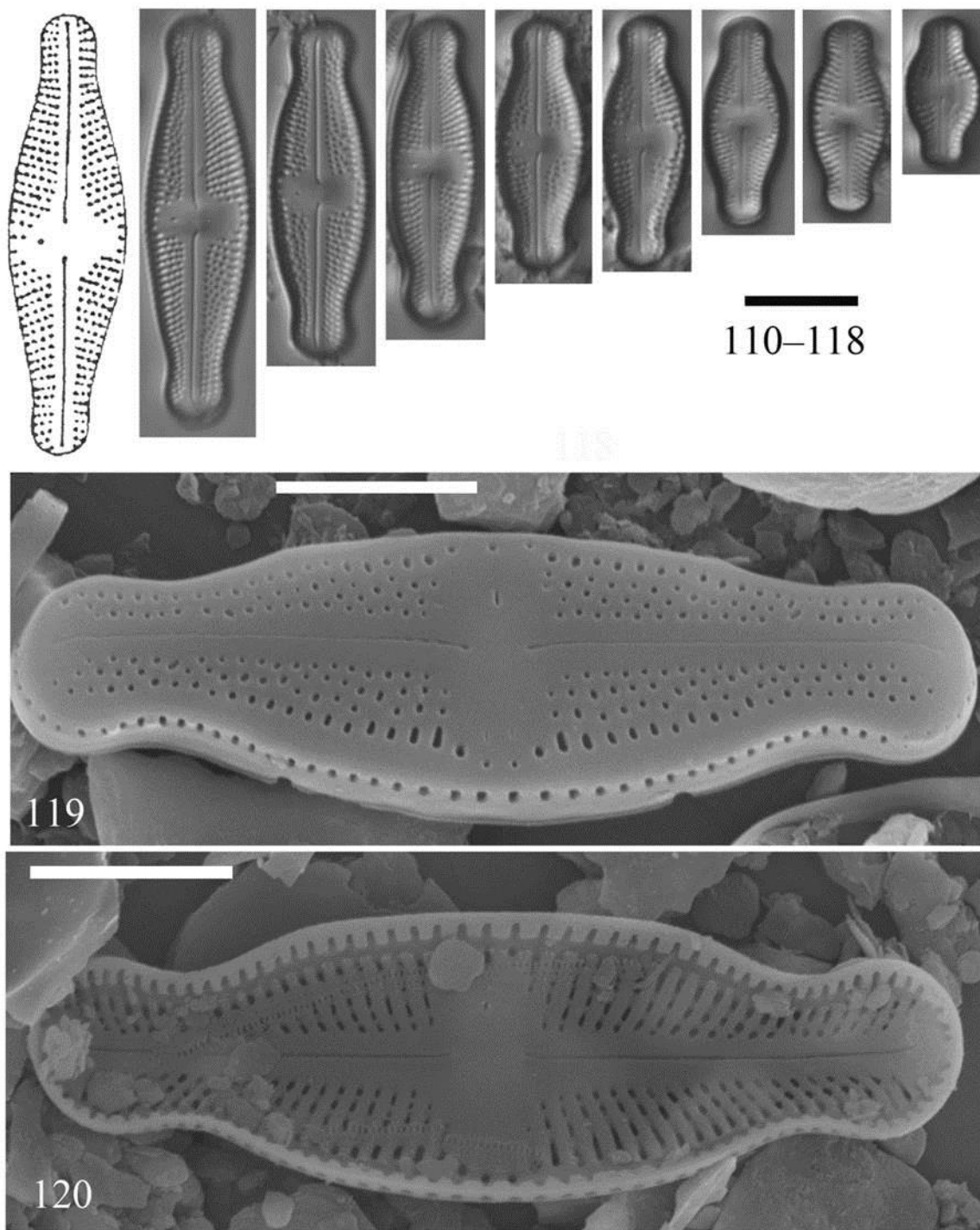
Observations:—If observed at all, the smaller size range of this species has probably been identified as *L. mutica* or *L. cohnii*, which may be a complex similar to *L. muticopsis* in Antarctica (Van de Vijver and Mataloni 2008). Like the lower size range of *L. spainiae*, *L. mutica* is oval-shaped, but the latter has eccentric proximal raphe endings terminating in hooks (Levkov et al. 2013: 284, pl. 2, figs. 1–8), which is visible under SEM. Furthermore, at the upper size ranges, *L. spainiae* has distinctly rostrate apices not present in *L. mutica*, and reaches a greater upper size (vs. 28 μm for *L. mutica*). *Luticola cohnii* is another diatom reported from the Antarctic continent that resembles *L. spainiae* in valve outline, especially at lower size ranges. However, *L. cohnii* is in general longer (19–40 μm) and wider (8.5–11.0 μm) than *L. spainiae* (Levkov et al. 2013: 91). Furthermore, *L. cohnii* is always oval in outline even at large sizes,

while valve apices become rostrate in *L. spainiae*. Furthermore, the eccentric distal raphe endings in *L. cohnii* terminate on valve margins, whereas in *L. spainiae*, they terminate on the valve face (Levkov et al. 2013: 292, pl. 6, figs. 1–8).

Other Antarctic diatoms such as *L. vermeulenii* (Van de Vijver et al. 2011: 145, figs. 16–29) may be similar in valve outline, but have a greater length and width range (24–50 μm , 9.5–14.0 μm). *Luticola vermeulenii* also has denser striae (14–17 in 10 μm vs. 19–22 in 10 μm) and differs in valve outline, never forming constrictions at the apices like the subcapitate endings in *L. spainiae* at upper size ranges. In the MDVs, *L. spainiae* is very similar in valve outline to *L. bradyi*, which is found in the same cryoconites. The major difference between these species is the width of valves. The upper end of the *L. spainiae* width range is 8.7 μm , while the lower width range of observed *L. bradyi* is 10.5 μm . Distal and proximal raphe pores are much larger in this species than in *L. bradyi*, which actually has a proximal raphe that resolves into slits. Also very similar is *L. laeta*, and it is possible that confusion between these two species has taken place in the past, as they are almost identical in their length/width ratios. However, *L. spainiae* has much broader, more rostrate apices than *L. laeta*, and has more areolae per striae, especially with regard to the shortened striae near the isolated pore in the central area, which only numbers 1–2 in *L. laeta*.

Luticola elegans* (W & G.S.West) Kohler & Kopalová, *comb. nov. stat. nov. (Figs 110–120, Fig. 110 is original illustration by West and West (1911)).

Basionym: *Navicula* (*Pinnularia*) *murrayi* var. *elegans* W. & G.S.West (1911) *British Antarctic Expedition 1907–1909, vol. 1., Biology, Part VII*, p. 285, pl. XXVI, fig. 130)



Figures 110–120. *Luticola elegans* (W. & G.S.West) Kohler & Kopalová, *comb. et stat. nov.* 109. Original illustration from West and West (1911: pl. 26, fig. 130). Light (LM) and scanning electron micrographs (SEM). 111–118. Specimens from Green Lake, Cape Royds, LM. 119. External valve view of a specimen from Green Lake, SEM. 120. Internal valve view of a specimen from the Nussbaum Riegel, SEM. LM scale bar = 10 μm . SEM scale bars = 5 μm .

Original description from West & West (1911): “*Var. minor, polis valvae angustioribus, productis et subcapitatis; striis 15 in 10 μ . Long. 31 μ ; lat. 8.1 μ .*”

LM observations:—(Figures 111–118) Valve lanceolate to elliptical-lanceolate with two convex margins. Apices capitate to sub-capitate in middle size ranges (Figures 112–115), becoming rostrate in smaller and greater size range (Figures 111, 116–118). Valve dimensions (n=10): length 12.9–35.8 μ m, width 6.4–9.5 μ m. Axial area linear, widening slightly towards central area. An isolated pore is present in the central area, located halfway between the valve margin and valve center. Central area broadly rectangular to round, bordered by shortened striae on both sides. Raphe branches straight, both proximal and distal raphe endings deflected away from the isolated pore. Transapical striae irregular, radiate throughout, 16–20 in 10 μ m.

SEM observations:—(Figures 119–120) Externally (Figure 119), striae composed of 3–4 areolae, 2–3 at apices. Areolae rounded throughout, becoming elongated at margins near central area, extend to the distal raphe ending. Isolated pore elongated, slit-like. Central area bordered by a single row of 3-4 rounded areolae on both sides, positioned closer to the valve margin than other striae. Distal raphe endings deflect away from isolated pore on a valve face, resolving into slits. Proximal raphe ending terminates in slightly opened pore, deflected away from isolated pore. Clear separation between valve face and margins, with open area at apices around terminal raphe endings. A single row of areolae visible in a shallow depression along entire valve mantle. Internally (Figure 120), structures difficult to discern due to specimen corrosion and small sample size.

Habitat, ecology and distribution:—*Luticola elegans* is known only from Cape Royds and the McMurdo Dry Valleys. Since this species has probably been identified as both *L. muticopsis* and *L. austroatlantica* due to similarities in morphology and extensive varieties present in *L.*

muticopsis (i.e. Ko-Bayashi 1963, 1965), its distribution may be more widespread than currently known. Sakaeva (2014) report it from many of the upland ponds from both Cape Royds and the MDVs, and we can confirm its presence in at least Wales and Crescent streams. The basionym, *Navicula murrayi* var. *elegans*, has been reported from Graham Land (Carlson 1913), Ongul Islands (Ko-Bayashi 1963), and South Shetland Islands (Carlson 1913), though these distributions should be interpreted with caution.

INSTAAR herbarium:—Green Lake 2475; Spaulding Pond 2495–2496; Blue Lake 2497–2499; Clear Lake 2501; McMurdo Hut Ridge 2664–2665; Picture Pond 2666–2668, 2670; Nussbaum Regal Pond (unofficial name) 2671; Upland Pond 2677–2678; Hughes Glacier Pond (unofficial name) 2679.

Observations:—West and West (1911) described *Navicula murrayi* var. *elegans* from presumably one large valve measuring 31 μm long, 8.1 μm wide, and with 15 striae per 10 μm . Later, Ko-Bayashi (1963: pl. 8, figs. 3–4) published images of what may be this diatom under the name *N. muticopsis* var. *elegans*, but it has been seldom reported since. In our survey of recent material at Cape Royds, we found a species that we argue belongs to *N. murrayi* var. *elegans* due to the strong morphological resemblance of the upper size range to the original illustration, as well as the locality from which our samples were taken. As a result, we here elevate the Cape Royds taxon to a species of *Luticola*. Levkov et al. (2013) report a species that may be conspecific from Cape Royds as *L. murrayi*, and has a length 16–35 μm , width 6.5–8.5 μm , and 15–17 striae in 10 μm . The authors also report initial cells up to 45 μm long and 12 μm wide. While we did not measure any initial cells of this length when analyzing the Mt. Erebus Moraine slides (including the lectotype, BM 34126), we did photograph one initial cell from BM 34124, and have included it as Fig. 57 for reference.

The upper size range of this species may be confused with *L. murrayi*, and is probably why this species was initially described as a variety. However, when a size diminution series of each species is observed and compared, they can be easily separated into two morphologically distinct groups. The morphology of *L. elegans* includes strongly capitate ends at intermediate size range, becoming more rostrate at the upper and lower size ranges. Apices of *Luticola murrayi* on the other hand never become capitate nor rostrate at upper or lower size ranges, and remain obtuse and rounded in all cells. Furthermore, the center of the valve remains rounded and convex in *L. elegans*, conforming well to the description of *Navicula murrayi* var. *elegans* reported by West and West (1911: fig. 130), while the widest part of *L. murrayi* is directly in the center of the cell. Lastly, the central stauros in *L. elegans* can be rounded (though it can also be rectangular) unlike *L. murrayi*, and is clearly illustrated in the original West and West (1911: fig. 130) illustration.

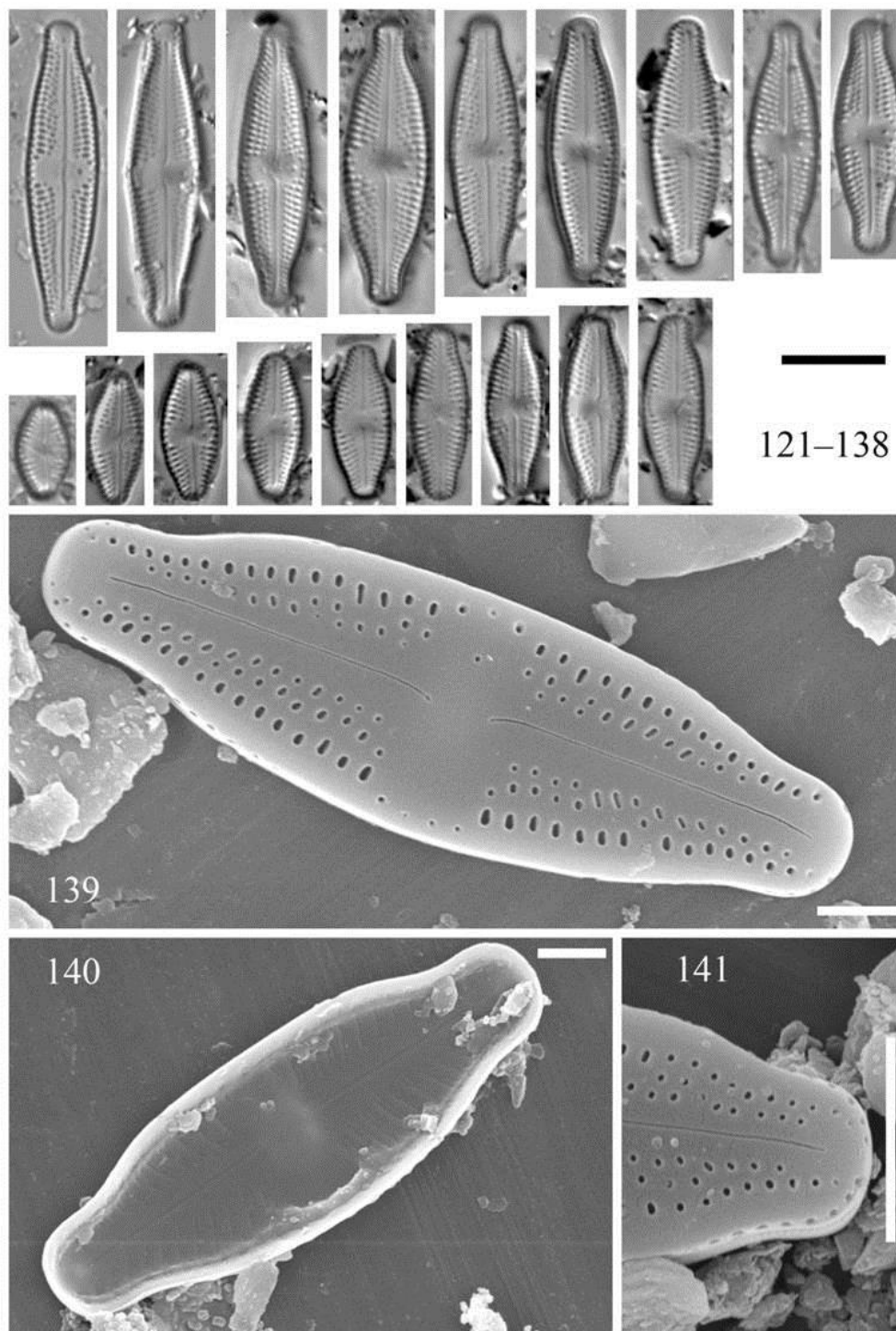
Luticola elegans may be confused with *L. austroatlantica*, which is very similar in valve outline at intermediate size ranges. However, *L. austroatlantica* is more narrow in width (5.6–8.2 μm vs. 6.4–9.5 μm), and has fewer areolae per striae (2–3 vs. 3–4). *Luticola elegans* additionally is less constricted between the capitate apices and the valve center compared to *L. austroatlantica*, and apices are generally wider. At the upper size range, *L. elegans* is more rostrate, while *L. austroatlantica* is more capitate. Conversely, *L. austroatlantica* is more rostrate at lower size ranges, while *L. elegans* has sub-capitate apices even at the smallest sizes. *Luticola elegans* may also resemble *L. gaussii*, and the two are often found in the same habitats, especially at Cape Royds. However, *L. gaussii* differs in valve outline, having a more rounded central portion while *L. elegans* is more elongate. In general, *L. gaussii* is wider and shorter than

L. elegans, and *L. gaussii* additionally has more dense (19–23 in 10 μm), patterned striae organized into three longitudinal rows not present in *L. elegans*.

***Luticola macknightiae* Kohler & Kopalová, *sp. nov.* (Figures 121–141)**

LM observations (Figures 121–138): Valves linear-lanceolate to elliptical-lanceolate, with convex, sometimes slightly undulate margins (Figures 122–123). Apices irregular protracted, nearly round, truncate to rostrate at smaller sizes (Figures 130–138). Valve dimensions (n=24): length 6.7–29.5 μm , width 4.3–7.8 μm . Axial area linear, widening towards the central area. An isolated pore present in the central area, located halfway between valve margin and valve center. Central area broadly elliptical, bordered on both sides by shortened striae. Raphe branches straight, with proximal and distal endings deflected opposite the isolated pore. Distal raphe endings short, terminating on the valve face well before apices. Transapical striae radiate throughout, 16–21 in 10 μm .

SEM observations (Figures 139–141): Externally (Figure 139), striae composed of 2–3 areolae, 1–2 at apices. Areolae rounded, elongated near valve margin, extend well past distal raphe endings before terminating almost on valve margin (Figure 141). Isolated pore rounded. Central area bordered on both sides by a single row of 3–4 rounded areolae positioned closer to the valve margin than other striae. Proximal raphe endings deflected opposite side of isolated pore, terminating into small open pores. Distal raphe endings straight, slightly deflected away from isolated pore, terminating into small fissures on the valve face distinctly before apices. Clear separation between valve face and margin, with clear open area at apices. A single row of rounded areolae visible along entire valve mantle. Internally (Figure 140), central nodule thickened. Marginal canal well developed, clearly visible in central area, interrupted at the



Figures 121–141. *Luticola macknightiae* Kohler & Kopalová, *sp. nov.* Light (LM) and scanning electron micrographs (SEM). 121–138. Specimens from Wormherder Creek, Taylor Valley, the type population, LM. 139. External valve view of a specimen from Canada Stream, Taylor Valley, SEM. 140. Internal valve view of a specimen from Canada Stream, SEM. 141. Detail of apices from Canada Stream specimen, SEM. LM scale bar = 10 µm. SEM scale bars = 2 µm for inside/outside, 5 µm for detail of external apice.

apices. Areolae covered by hymenes, forming continuous a strip along each stria. Isolated pore opening covered by solid silica flap.

Type:—ANTARCTICA. McMurdo Dry Valleys: Taylor Valley, Wormherder Creek microbial mat, Sample WHC11-2, *T.J. Kohler*, 10 January 2012 (holotype INSTAAR! #958, illustrated in Fig. 125, isotypes BM! 101778, BR! 4407).

Etymology:—*Luticola macknightiae* is named in honor of our advisor, colleague, and friend, Dr. Diane McKnight (University of Colorado, Boulder, USA), who has promoted a better understanding of freshwater ecosystems through her research in the McMurdo Dry Valleys.

Habitat, ecology and distribution:—At present, *L. macknightiae* is only known from the McMurdo Dry Valleys. As it has been previously been identified as *L. muticopsis* f. *evoluta* (Esposito et al. 2006, 2008, Spaulding et al. 2010, Stanish et al. 2011, 2012), its distribution is known to be widespread throughout the MDVs, occupying stream microbial mats and mosses. It is especially abundant in the Lake Bonney Basin streams, where it sometimes comprises half of the communities by relative abundance (Stanish et al. 2012).

INSTAAR herbarium:—Aiken Creek 900, 2227; Von Guerard Stream 906–907, 911–912, 916–917, 919, 923–926; Harnish Creek 928; Bowles Creek 933, 936, 938, 940; Commonwealth Stream 945, 948; Wormherder Creek 955, 958; Priscu Stream 960–961; Bohner Stream 963–966; McKay Creek 975, 977; Wharton Creek 979–980, 982; Delta Stream 983–984, 986–987, 990–992; Onyx River 995–996, 999; Canada Stream 1003, 1011, 2257; Green Creek 1018–1019, 1021–1022, 1025, 1027; Lawson Creek 1030, 1032–1033; Miers Stream 1049; Adams Stream 1051–1054, 1064; Relict Channel 1068, 1070, 1077–1081, 1084, 1087; Little Sharpe (unofficial name) 2340; Lyons Stream tributary 2349–2351; Spaulding Pond 2495–2496; Blue Lake 2498;

Clear Lake 2501; McMurdo Hut Ridge 2665; Picture Pond 2667–2670; Nussbaum Regal Pond (unofficial name) 2671, Upland Pond 2677–2678.

Observations:—The identification of *L. macknightiae* as *N. muticopsis* f. *evoluta* probably originates with the publication by Ko-Bayashi (1965: pl. 31), where a small *Luticola* with almost rostrate apices is depicted as this form. Since there is no illustration of *N. muticopsis* f. *evoluta* in West and West (1911), and the original description is limited to “Cells are slightly elongated, slightly below the pole, each distinct but slightly constricted; striae 13–14 in 10 μm ” (translated from Latin, West and West 1911: 283), it is entirely impossible to match this form with any extant species. Because of this, *N. muticopsis* f. *evoluta* has previously been identified as what is the current concept for *L. austroatlantica* (Kellogg 1980: 176, pl. 1, fig.11), *L. pseudomurrayi* (Ko-Bayashi 1963: pl. 8, figs. 1–2), and the reduced form of various unknown diatoms (Ko-Bayashi 1965: pl. 29). Furthermore, in our investigation of the recent Cape Royds material, as well as the original slides from Shackleton’s expedition, we found no valves resembling *L. macknightiae*, although West and West (1911: 284) stated that *N. muticopsis* f. *evoluta* was “...common over the whole area in which collections were made”. Because of its absence, we conclude the two are not conspecific, and we describe *L. macknightiae* as a new species.

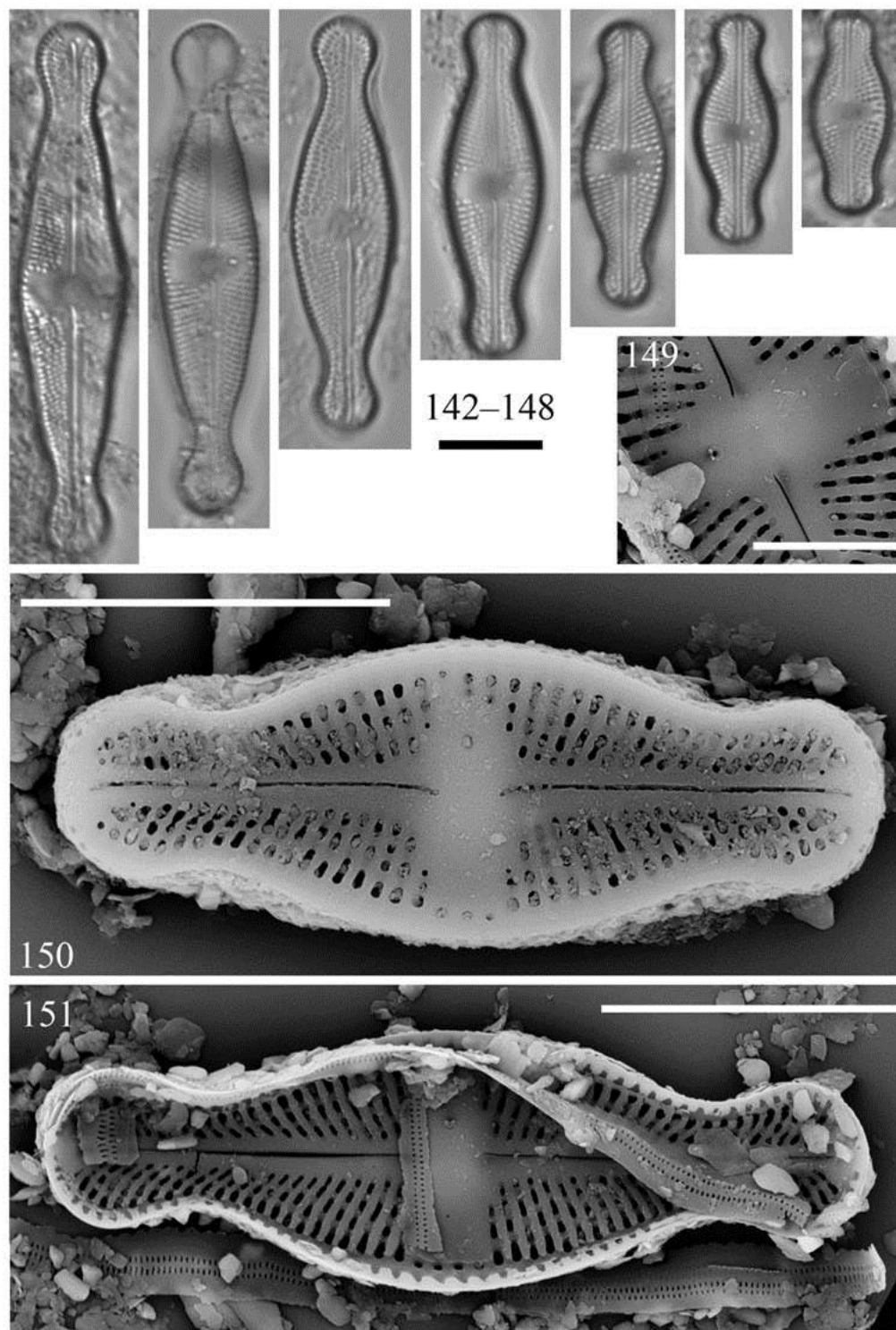
Luticola macknightiae most resembles *L. vesnae* Levkov in Levkov et al. (2013: 254, pl. 15, figs. 5–6, and pl. 157, figs. 13–21) valve outline. Described from Macedonia, *L. vesnae* is similar in size, measuring 17–34 μm long and 5.3–8.0 μm wide (Levkov et al. 2013). However, it has more dense striae (22–24 in 10 μm), more areolae per stria (3 or 4), and external distal raphe endings continue onto valve mantle, whereas in *L. macknightiae* the raphe terminates at or before the last row of areolae. Among Antarctic taxa, *L. macknightiae* shares similarities to *L. delicatula* Van de Vijver, Kopalová, Zidarova & Levkov in Levkov et al. (2013: 99, pl. 53, figs

21–26, pl. 54, fig. 6), though this species is wider (7.0–9.0 μm), has more coarse striae (15–16 in 10 μm), and is generally widest in the center of the valve tapering to rounded apices. This is in contrast to *L. macknightiae* which has two convex margins and rostrate apices. *Luticola macknightiae* may also resemble *L. pusilla* Van de Vijver, Kopalová, Zidarova & Levkov in Levkov et al. (2013: 203, pl. 50, figs. 1–16, pl. 51, figs. 1–7) in dimensions; *L. pusilla* is 12–28 μm long, 4.5–7.5 μm wide, and has 18–21 striae in 10 μm composed of 2–3 areolae. It differs from *L. macknightiae* in having more rounded apices and a more oval shaped intermediate size range. Furthermore, *L. pusilla* has a widened distal end of the raphe not present in *L. macknightiae* (Levkov et al. 2013).

On continental Antarctica, *L. macknightiae* may only be confused with *L. austroatlantica* because both taxa have convex margins and at intermediate size ranges exhibit rostrate apices. However, *L. austroatlantica* has distinctly capitate apices at upper size ranges and are more parallel where they meet the central are in intermediate size ranges resulting in distinct “shoulders”. In *L. macknightiae*, apices are rostrate at intermediate sizes, and are never fully capitate at upper size ranges. In addition, the areolae of *L. macknightiae* are more sparsely distributed within striae (2–3) compared with *L. austroatlantica* (3–4). Lastly, *L. macknightiae* is consistently narrower than *L. austroatlantica* at any given length, making comparisons between populations straightforward.

***Luticola transantarctica* Kohler & Kopalová, sp. nov. (Figures 142–151)**

LM observations (Figures 142–148): Valves elliptic-lanceolate, becoming slightly rhombic in larger specimens (Figures 142–143). Margins symmetrical, convex and rounded in central area. Apices broadly rounded, capitate, becoming slightly rostrate in smaller specimens (Figure 148).



Figures 142–151. *Luticola transantarctica* Kohler & Kopalová, *sp. nov.* Light (LM) and scanning electron micrographs (SEM). 142–148. Specimens from the Labyrinth Pond, Wright Valley, the type population, LM. 149. Detail of isolated pore, internal valve view, SEM. 150. External valve view, type population, SEM. 151. Internal valve view, type population, SEM. LM scale bar = 10 μm . SEM scale bars = 10 μm , 4 μm for detail of internal isolated pore.

Valve dimensions (n=25): length 16.0–50.9 μm , width 7.1–10.6 μm . Axial area narrow, expanding towards central area. An isolated pore present in central area, located halfway between valve center and valve margin. Central area rectangular to elliptical, bordered by shortened striae on both sides. Raphe branches straight with both proximal and distal endings slightly deflecting away from isolated pore. Transapical striae radiate throughout, 18–22 in 10 μm .

SEM observations (Figures 149–151): Externally (Figure 150), striae composed of 3–5 areolae, 2–3 at apices. Areolae rounded to elongated throughout, extending to the distal raphe endings. Isolated pore appears slightly elongated, but obscured by debris. Central area bordered by 1–2 rows of three rounded areolae on the isolated pore side, and a single row on the opposite side. Proximal and distal raphe endings slightly deflected opposite isolated pore, terminate on valve face. Clear separation between valve face and margins. A single row of rounded areolae visible along valve mantle, interrupted at apices. Internally (Figures 149, 151), structures difficult to discern due to specimen corrosion and small sample size. Central nodule thickened. Distal raphe endings straight, proximal raphe endings deflect slightly towards isolated pore.

Type:—ANTARCTICA, McMurdo Dry Valleys, Wright Valley, Labyrinth Pond, Sample #4, A. Sakaeva, 07 January 2014 (holotype INSTAAR! #2669, illustrated in Fig. 145, isotypes BM! 101779, BR! 4408)

Etymology:—The name “*transantarctica*” is in reference to the isolated locality in which the type population was collected from; The Labyrinth, Wright Valley, at the foot of the Transantarctic Mountains.

Habitat, ecology and distribution:—At present, this species is only known from The Labyrinth in Wright Valley, Antarctica, where it comprised over 60% of the diatom community by relative abundance (Sakaeva 2014).

INSTAAR herbarium:—Labyrinth Pond 2669.

Observations:—If observed at all, the lower size range of this taxon may have previously been identified as *L. muticopsis* f. *reducta* because of images published by Kellogg et al. (1980), which appear to show the reduced form of *L. gaussii* or other *Luticola* with rounded apices. Like *N. muticopsis* f. *evoluta*, there is no original illustration for *L. muticopsis* f. *reducta*, and the description is limited to “Cells are shorter, poles less drawn out and distinctly truncated, striae 13 in 10 μ ” (translated from Latin, West and West 1911: 284). However, since *L. transantarctica* was not observed in our survey of Cape Royds, nor in the original West and West (1911) slides, we conjecture that the two are not conspecific. Based on published images, it is also possible that *L. transantarctica* has been observed in the past and identified as *L. murrayi* (Kellogg et al. 1980: 176, pl. 1, fig.20) or *Naviula globiceps* f. *amphicephala* (Ko-Bayashi 1963: 13, pl. 4, fig. 3), but these populations should be re-investigated before this can be said for certain.

From the Antarctic continent, *Luticola transantarctica* is most similar in morphology to *L. pseudomurrayi*, described from Langhovde, Lützow Holm Bay, East-Antarctica (Van de Vijver et al. 2012). However, *L. transantarctica* differs from *L. pseudomurrayi* by having more capitate apices, with narrower constrictions between the apices and the valve center. Lastly, *L. pseudomurrayi* has a larger upper width range than *L. transantarctica* (7.5–12.0 μ m vs. 7.1–10.6 μ m). From the McMurdo Sound Region, *L. transantarctica* could be confused with *L. elegans*, especially at the lower end of the size range. However, apices in *L. transantarctica* remain

capitate at small sizes, whereas in *L. elegans* they become more rostrate at lower as well as greater sizes. *Luticola gaussii* is very similar in valve outline, especially at intermediate lengths. However, *L. gaussii* has a more rounded central area compared to the elliptic central area in *L. transantarctica*, and *L. gaussii* additionally has slitted punta under SEM. Furthermore, the striae of *L. gaussii* are patterned as noted by West and West (1911), with two lines running along the axial area in the valve center and one at the apices. In *L. transantarctica*, striae form no such pattern, are punctate and irregular. Finally, *L. gaussii* is consistently wider than *L. transantarctica* at any given length.

DISCUSSION

Based on the results of this study and recent literature (Table 2), our observations indicate the presence of 43 different *Luticola* taxa confirmed from the Antarctic Region. Following the application of a more fine-grained taxonomy, almost 98 % of all *Luticola* species within this grouping are restricted to the Antarctic Region, with a majority (53 %) confirmed only from the Maritime Antarctic. Furthermore, 21 % are known only from the Antarctic continent, and 14 % are typically present only in the sub-Antarctic region. The results also reveal that less than 10 % of the total number of observed species (*L. austroatlantica*, *L. permuticopsis*, *L. gaussii*, and *L. muticopsis*) is shared between the Antarctic continent and Maritime Antarctic Region (MA/CA, not counting *L. cohnii*). There is no evidence for a species only shared between the sub-Antarctic and the Antarctic continent without being also present in the Maritime Antarctic Region, and there is no species that is shared exclusively between the sub- and Maritime Antarctic. Only one species, *L. muticopsis*, is present across the entire Antarctic Region. These results are in strong contrast to previous reports of the biogeographical features of the Antarctic diatom flora, where a

Table 2. Distribution of *Luticola* species recorded during this study and those taken from the literature with assigned biogeographic regions defined by Chown and Convey (2007). SA = sub-Antarctic Region, MA = Maritime Antarctic Region, CA = Continental Antarctic Region.

Taxon	Distribution
<i>Luticola cohnii</i> (Hilse) D.G.Mann	C
<i>Luticola dolia</i> Spaulding & Esposito	CA
<i>Luticola elegans</i> (West & West) Kohler & Kopalová	CA
<i>Luticola laeta</i> Spaulding & Esposito	CA
<i>Luticola macknightiae</i> Kohler & Kopalová	CA
<i>Luticola murrayi</i> (West & West) D.G.Mann	CA
<i>Luticola pseudomurrayi</i> Van de Vijver & Tavernier	CA
<i>Luticola spainiae</i> Kohler & Kopalová	CA
<i>Luticola bradyi</i> Kohler	CA
<i>Luticola transantarctica</i> Kohler & Kopalová	CA
<i>Luticola adelae</i> Van de Vijver & Zidarova	MA
<i>Luticola amoena</i> Van de Vijver, Kopalová, Zidarova & Levkov	MA
<i>Luticola australomutica</i> Van de Vijver	MA
<i>Luticola bogaertsiana</i> Zidarova, Levkov & Van de Vijver	MA
<i>Luticola caubergsii</i> Van de Vijver	MA
<i>Luticola contii</i> Zidarova, Levkov & Van de Vijver	MA
<i>Luticola delicatula</i> Van de Vijver, Kopalová & Zidarova	MA
<i>Luticola desmetii</i> Kopalová & Van de Vijver	MA
<i>Luticola doliiformis</i> Kopalová & Van de Vijver	MA
<i>Luticola evkae</i> Kopalová	MA
<i>Luticola gigamuticopsis</i> Van de Vijver	MA
<i>Luticola higleri</i> Van de Vijver, Van Dam & Beyens	MA
<i>Luticola katkae</i> Van de Vijver & Zidarova	MA
<i>Luticola neglecta</i> Zidarova, Levkov & Van de Vijver	MA
<i>Luticola nelidae</i> Van de Vijver	MA
<i>Luticola olegsakharovii</i> Zidarova, Levkov & Van de Vijver	MA
<i>Luticola pusilla</i> Van de Vijver, Kopalová, Zidarova & Levkov	MA
<i>Luticola quadriscribiculata</i> Van de Vijver in Van de Vijver & Mataloni (2008: 457, figs 18-28)	MA
<i>Luticola raynae</i> Zidarova & Van de Vijver in Van de Vijver et al. (2011: 150, figs 52-62)	MA
<i>Luticola tomsui</i> Kopalová in Kopalová et al. (2011: 56, figs 73-87)	MA
<i>Luticola truncata</i> Kopalová & Van de Vijver	MA
<i>Luticola vandeijveri</i> Kopalová, Zidarova & Levkov	MA
<i>Luticola vermeulenii</i> Van de Vijver	MA
<i>Luticola austroatlantica</i> Van de Vijver, Kopalová, Spaulding & Esposito	MA/CA
<i>Luticola gaussii</i> (Heiden) D.G.Mann	MA/CA
<i>Luticola permuticopsis</i> Kopalová & Van de Vijver	MA/CA
<i>Luticola muticopsis</i> (Van Heurck) D.G.Mann	MA/CA/SA
<i>Luticola beyensii</i> Van de Vijver, Ledeganck & Lebouvier in Van de Vijver et al. (2002: 236, figs 2-13)	SA
<i>Luticola crozetensis</i> Van de Vijver, Kopalová, Zidarova & Levkov in Levkov et al. (2013: 94, pl. 46, figs 1-14)	SA
<i>Luticola ledeganckii</i> Van de Vijver in Van de Vijver et al. (2002: 56-57, pl. 57, figs 7-14)	SA
<i>Luticola robusta</i> Van de Vijver, Ledeganck & Beyens in Van de Vijver et al. (2002: 59, pl. 58, figs 1-7)	SA
<i>Luticola subcrozetensis</i> Van de Vijver, Kopalová, Zidarova & Levkov in Levkov et al. (2013: 228, pl. 46, 15-31)	SA
<i>Luticola suecorum</i> (Carlson 1913: 15, figs 1-27) Van de Vijver in Van de Vijver & Mataloni (2008: 467)	SA

majority of the species was considered to be cosmopolitan (Jones 1996, Van de Vijver and Beyens 1999, Toro et al. 2007, Esposito *et al.* 2008, Vinocur and Maidana 2010).

Only *L. cohnii* has a cosmopolitan distribution in our analysis, but it is not clear that records report the genuine *L. cohnii*. Although commonly reported from the entire Antarctic

Region, including the continent, we found no valves that could be identified conclusively as *L. cohnii* or the similar *L. mutica*. Like many *Luticola* species previously force-fitted into European taxa, these species may be over-reported due to their typical, rounded valve outlines. Following the MacDonald-Pfitzer rule of size diminution (Round et al. 1990), diatoms often lose their defining shape characteristics at their lower size ranges, and some species (such as *L. laeta* and *L. spainiae*) become more rounded as they become smaller. This, along with the application of a too broad species concept, may result in an inability to separate these reduced valves from familiar European taxa such as *L. mutica* and *L. cohnii*. It follows that caution should be taken in considering *L. cohnii* a cosmopolitan diatom until more studies utilizing SEM for the defining morphological characters, and ultimately molecular approaches, can verify its ubiquity.

In our investigation of both recent and original material derived from Cape Royds, we did not find any species that we would attribute to *Navicula muticopsiforme*, *N. muticopsis* f. *evoluta*, or *L. muticopsis* f. *reducta*, all of which were newly described by West and West (1911). While an illustration for *N. muticopsiforme* is presented in the paper to aid in making an identification, there are unfortunately no illustrations for *N. muticopsis* f. *evoluta* nor *L. muticopsis* f. *reducta*, and only modest descriptions. Furthermore, the latter two formae do not have size ranges, and only include overlapping stria densities (13–14 vs. 13 in 10 μm). Because these new forms can neither be identified nor distinguished between each other, we would discourage their use as taxonomic entities, and we conjecture that these likely belong to the smallest cells in the cell cycles of other *Luticola* taxa (Van de Vijver et al. 2012, Levkov et al. 2013), rather than separate entities in their own right.

Lastly, we failed to observe any specimen of *L. pseudomurrayi* in this survey from the McMurdo Sound Region, although it has previously been documented from other parts of East

Antarctica (Ko-Bayashi 1963, Roberts and McMinn 1999, Sabbe et al. 2003, Ohtsuka et al. 2006, Van de Vijver et al. 2012). While this diatom may very well be present in the McMurdo Sound Region, it cannot be verified at this time. However, it is interesting that it is often found amongst other genera that have yet to be observed in the McMurdo Sound Region, such as *Gomphonema*, *Pseudostaurosira*, and *Stauroforma* (Sabbe et al. 2003) among others (Roberts and McMinn 1999). Because of this, patterns delineating the Antarctic continent flora may be more complex than the single category adapted from Chown and Convey (2007) suggests. We conclude that the genus *Luticola* is highly endemic in continental Antarctica, distinct from the sub- and Maritime Antarctic Regions, and may serve as a fruitful model organism for studying microbial biogeography.

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REFERENCES

- Baker, A.N. 1967. Algae from Lake Miers, a solar-heated Antarctic lake. *New Zealand Journal of Botany* 5: 453–468. doi: 10.1080/0028825X.1967.10428767
- Ball, B.A., and Virginia, R.A. 2014. The ecological role of moss in a polar desert: implications for aboveground–belowground and terrestrial–aquatic linkages. *Polar Biology* 37: 651–664. doi: 10.1007/s00300-014-1465-2
- Carlson, G.W.F. 1913. Süßwasseralgae aus der Antarktis, Südgeorgien und den Falkland Inseln. *Wissenschaftliche Ergebnisse der Schwedischen Südpolar-Expedition 1901–1903, unter leitung von dr. Otto Nordenskjöld*: 4 (Botanique):1–94.
- Chown, S.L., and Convey, P. 2007. Spatial and temporal variability across life’s hierarchies in the terrestrial Antarctic. *Philosophical Transactions of the Royal Society B* 362: 2307–2331. doi: 10.1098/rstb.2006.1949
- Esposito R.M.M., Horn, S.L., McKnight, D.M., Cox, M.J., Grant, M.C., Spaulding, S.A., Doran, P.T. and Cozzetto, K.D. 2006. Antarctic climate cooling and response of diatoms in glacial meltwater streams. *Geophysical Research Letters* 33: L07406.1–L07406.4. doi: 10.1029/2006GL025903.
- Esposito, R.M.M., Spaulding, S.A., McKnight, D.M., Van de Vijver, B., Kopalová, K., Lubinski, D., Hall, B., and Whittaker, T. 2008. Inland diatoms from the McMurdo Dry Valleys and James Ross Island, Antarctica. *Canadian Journal of Botany* 86: 1378–1392. doi: 10.1139/B08-100.
- Fritsch, F.E. 1912. Freshwater algae. National Antarctic “Discovery” Expedition 1901–1904. *British Museum of Natural History* 6: 1–66.
- Fukushima, H. 1964. Diatoms vegetation on ice-free area of Cape Royds, Antarctica. *Antarctic Record* 22: 1–13.
- Fukushima, H. 1966. Diatoms from Molodezhnaya Station and Mirny Station, Antarctica. *Antarctic Record* 27: 13–17.
- Fukushima, H., Watanuki, T., and Ko-bayashi, T. 1973. A preliminary report on the diatoms from East Ongul Island. *Antarctic Record* 46: 125–132.
- Fukushima, H., Watanuki, T., and Ko-bayashi, T. 1974. Diatoms from O-ike, West Ongul Island, Antarctica. *Antarctic Record* 50: 35–40.

- Gregory, W. 1856. Notice of some new species of British fresh-water Diatomaceae. *Quarterly Journal of Microscopical Science* 4: 1–14.
- Heiden, H., and Kolbe, R.W. 1928. Die marinen Diatomeen der Deutschen Südpolar-Expedition 1901-1903. *Deutsche Südpolar-Expedition 1901–1903* 8/5 (botanik): 447–715.
- Hustedt, F. 1966. Die Kieselalgen Deutschlands, Österreichs und der Schweiz unter Berücksichtigung der übrigen Länder Europas sowie der angrenzenden Meeresgebiete. In Rabenhorst, L., Ed. *Kryptogamen Flora von Deutschland, Österreich und der Schweiz*. (Teil 3, Lief. 4). Akademische Verlagsgesellschaft m.b.h., Leipzig, pp. 557–816.
- Jones, V.J. 1996. The diversity, distribution and ecology of diatoms from Antarctic inland waters. *Biodiversity and Conservation* 5: 1433–1449. doi: 10.1007/BF00051986
- Kellogg, T.B., and Kellogg, D.E. 2002. Non-marine and littoral diatoms from Antarctic and Sub-Antarctic regions. Distribution and updated taxonomy. *Diatom Monographs* 1: 1–795.
- Kellogg, D.E., Stuiver, M., Kellogg, T.B., and Denton, G.H. 1980. Non-marine diatoms from late Wisconsin perched deltas in Taylor Valley, Antarctica. *Paleogeography, Paleoclimatology, Paleocology* 30: 157–189.
- Ko-Bayashi, T. 1963. Variations on some pennate diatoms from Antarctica, 1. Japanese Antarctic Research Expedition 1956-1962, Scientific Reports, Series E, 18: 1–20.
- Ko-Bayashi, T. 1965. Variations on some pennate diatoms from Antarctica, 2. Japanese Antarctic Research Expedition 1956-1962, Scientific Reports, Series E, 24: 1–28.
- Konfirst, M.A., Sjunneskog, C., Scherer, R.P., and Doran, P.T. 2011. A diatom record of environmental change in Fryxell Basin, Taylor Valley, Antarctica, late Pleistocene to present. *Journal of Paleolimnology* 46: 257–272. doi: 10.1007/s10933-011-9537-6
- Kopalová, K., and Van de Vijver, B. 2013. Structure and ecology of freshwater benthic diatom communities from Byers Peninsula, Livingston Island, South Shetland Island. *Antarctic Science* 25: 239–253. doi: 10.1017/S0954102012000764
- Kopalová, K., Elster, J., Nedbalová, L., and Van de Vijver, B. 2009. Three new terrestrial diatom species from seepage areas on James Ross Island (Antarctic Peninsula Region). *Diatom Research* 24: 113–122. doi: 10.1080/0269249X.2009.9705786
- Kopalová, K., Nedbalová, L., de Haan, M., and Van de Vijver, B. 2011. Description of five new species of the diatom genus *Luticola* (Bacillariophyta, Diadesmidaceae) found in lakes of James Ross Island (Maritime Antarctic Region). *Phytotaxa* 27: 44–60.
- Kopalová, K., Veselá, J., Elster, J., Nedbalová, L., Komárek, J., and Van de Vijver, B. 2012. Benthic diatoms (Bacillariophyta) from seepages and streams on James Ross Island (NW

- Weddell Sea, Antarctica). *Plant Ecology and Evolution* 145:190–208. doi: 10.5091/plecevo.2012.639
- Kopalová, K., Nedbalová, L., Nývlt, D., Elster, J., and Van de Vijver, B. 2013. Diversity, ecology and biogeography of the freshwater diatom communities from Ulu Peninsula (James Ross Island, NE Antarctic Peninsula). *Polar Biology* 36: 933–948. doi: 10.1007/s00300-013-1317-5
- Kopalová, K., Ochyra, R., Nedbalová, L., and Van de Vijver, B. 2014. Moss-inhabiting diatoms from two contrasting Maritime Antarctic islands. *Plant Ecology and Evolution* 147: 67–84. doi: 10.5091/plecevo.2014.896
- Kützing, F.T. 1844. *Die Kieselchaligen. Bacillarien oder Diatomeen*. Nordhausen, 152 pp.
- Levkov, Z., Metzeltin, D. & Pavlov, A. (2013) *Luticola* and *Luticolopsis*. In Lange-Bertalot, H., Ed. *Diatoms of Europe: Diatoms of the European Inland Waters and Comparable Habitats*. Volume 7. Koeltz Scientific Books, Königstein, 698 pp.
- Lowe, R.L., Kociolek, P., Johansen, J.R., Van De Vijver, B., Lange-Bertalot, H., and Kopalová, K. 2014. *Humidophila* gen. nov., a new genus for a group of diatoms (Bacillariophyta) formerly within the genus *Diadesmis*: species from Hawai'i, including one new species. *Diatom Research* 29: 351–360. doi: 10.1080/0269249X.2014.889039
- McKnight, D.M., Niyogi, D.K., Alger, A.S., Bomblies, A., Conovitz, P.A., and Tate, C.M. 1999. Dry valley streams in Antarctica: ecosystems waiting for water. *Bioscience* 49: 985–995. doi: 10.1525/bisi.1999.49.12.985
- Ohtsuka, T., Kudoh S., Imura S., and Ohtani, S. 2006. Diatoms composing benthic microbial mats in freshwater lakes of Skarvsnes ice-free area, East Antarctica. *Polar Bioscience* 20: 113–130.
- Peragallo, M. 1921. *Diatomées d'eau douce. Première partie. Deuxième Expédition Antarctique Française (1908–1910) commandé par le Dr. J. Charcot. Ouvrage publié sous les auspices du Ministère de l'Institution publique*. Masson et Cie, Paris, pp. 1–38.
- Prescott, G.W. 1979. A contribution to a bibliography of Antarctic and Subantarctic algae: together with a checklist of freshwater taxa reported to 1977. *Bibliotheca Phycologica* 45: 1–312.
- Rabenhorst, L. 1860. *Die Algen Sachsens. Resp. Mittel-Europa's Gesammelt und herausgegeben von Dr. L. Rabenhorst*, Dresden, no. 962a.
- Roberts, D., and McMinn, A. 1999. Diatoms of the saline lakes of the Vestfold Hills, Antarctica. *Bibliotheca Diatomologica* 44: 1–82.

- Round, F.E., Crawford, R.M., and Mann, D.G. 1990. The diatoms: biology and morphology of the genera. Cambridge University Press, Cambridge, 760 pp.
- Sabbe, K., Verleyen, E., Hodgson, D.A., Vanhoutte, K., and Vyverman, W. 2003. Benthic diatom flora of freshwater and saline lakes in the Larsemann Hills and Rauer Islands, East Antarctica. *Antarctic Science* 15: 227–248. doi: 10.1017/S095410200300124X
- Sakaeva, A. 2014. Ecology and biogeography of freshwater diatoms in ponds of McMurdo Dry Valleys and parts of the Ross Island. Master's Thesis, University of Colorado.
- Seaburg, K.G., Parker, B.C., Prescott, G.W., and Whitford, L.A. 1979. The algae of southern Victoria Land. *Bibliotheca Phycologia* 46: 169.
- Spaulding, S.A., and Stoermer, E.F. 1997. Taxonomy and the distribution of the genus *Muelleria* Frenguelli. *Diatom Research* 12: 95–113. doi: 10.1080/0269249X.1997.9705405
- Spaulding, S.A., McKnight, D.M., Stoermer, E.F., and Doran, P.T. 1997. Diatoms in sediments of perennially ice-covered Lake Hoare, and implications for interpreting lake history in the McMurdo Dry Valleys of Antarctica. *Journal of Paleolimnology* 17: 403–420. doi: 10.1023/A:1007931329881
- Spaulding, S., Esposito, R., Lubinski, D., Horn, S., Cox, M., McKnight, D., Alger, A., Hall, B., Mayernick, M., Whittaker, T., and Yang, C. 2010. Antarctic Freshwater Diatoms web site, McMurdo Dry Valleys LTER. Available: <http://huey.colorado.edu/diatoms>
- Stanish, L.F., Nemergut, D.R., and McKnight, D.M. 2011. Hydrologic processes influence diatom community composition in Dry Valley streams. *Journal of the North American Benthological Society* 30: 1057–1073. doi: 10.1899/11-008.1
- Stanish, L.F., Kohler, T.J., Esposito, R.M.M., Simmons, B., Nielsen, U.N., Wall, D.H., Nemergut, D., and McKnight, D.M. 2012. Extreme streams: Hydrologic controls on diatom communities across a gradient of intermittent glacial meltwater streams in the McMurdo Dry Valleys, Antarctica. *Canadian Journal of Fisheries and Aquatic Sciences* 69: 1405–1419. doi: 10.1139/f2012-022
- Stanish, L.F., Bagshaw, E.A., McKnight, D.M., Fountain, A.G., and Tranter, M. 2013. Environmental factors influencing diatom communities in Antarctic cryoconite holes. *Environmental Research Letters* 8: 045006. doi: 10.1088/1748-9326/8/4/045006
- Toro, M., Camacho, A., Rochera, C., Rico, E., Bañón, M., Fernández-Valiente, E., Marco, E., Justel, A., Avendaño, M.C., Ariosa, Y., Vincent, W.F. and Quesada, A. 2007. Limnological characteristics of the freshwater ecosystems of Byers Peninsula, Livingston Island, in maritime Antarctica. *Polar Biology* 30: 635–649. doi: 10.1007/s00300-006-0223-5
- Tyler, P.A. 1996. Endemism in freshwater algae, with special reference to the Australian region. *Hydrobiologia* 336: 127–135. doi: 10.1007/978-94-017-0908-8_12

- Van de Vijver, B., and Beyens, L. 1999. Biogeography and ecology of freshwater diatoms in Subantarctica. *Journal of Biogeography* 26: 993–1000. doi: 10.1046/j.1365-2699.1999.00358.x
- Van de Vijver, B., Frenot, Y., and Beyens, L. 2002. Freshwater diatoms from Île de la Possession (Crozet archipelago, subantarctica). *Bibliotheca Diatomologica* 46: 1–412.
- Van de Vijver, B., Ledeganck, P., and Lebouvier, M. (2002) *Luticola beyensii* sp. nov., a new aerophilous diatom from île Saint Paul (Indian Ocean, TAAF). *Diatom Research* 17: 235–241. doi: 10.1080/0269249X.2002.9705541
- Van de Vijver, B., and Mataloni, G. 2008. New and interesting species in the genus *Luticola* D.G. Mann (Bacillariophyta) from Deception Island (South Shetland Islands). *Phycologia* 47: 451–467. doi: 10.2216/07-67.1
- Van de Vijver, B., Mataloni, G., Stanish, L. and Spaulding, S. A. 2010. New and interesting species from the genus *Muelleria* (Bacillariophyta) from the Antarctic region and South Africa. *Phycologia* 49: 22–41. doi: 10.2216/09-27.1
- Van de Vijver, B., Tavernier, I. Kellogg, T.B., Gibson, J., Verleyen, E., Vyverman, W. and Sabbe, K. 2012. Revision of type materials of Antarctic diatom species (Bacillariophyta) described by West & West (1911), with the description of two new species. *Fottea* 12: 149–169. doi : 10.1127/0029-5035/2011/0092-0137
- Van de Vijver, B., Van Dam, H., and Beyens, L. 2006. *Luticola higleri* sp. nov., a new diatom species from King George Island (South Shetland Islands, Antarctica). *Nova Hedwigia* 82: 69–79. doi: 10.1127/0029-5035/2006/0082-0069
- Van de Vijver, B., Zidarova, R. and de Haan, M. 2011. Four new *Luticola* taxa (Bacillariophyta) from the South Shetland Islands and James Ross Island (Maritime Antarctic Region). *Nova Hedwigia* 92: 137–158. doi: 10.1127/0029-5035/2011/0092-0137
- Van Heurck, H. 1909. Diatomées. Résultats du Voyage du S.Y. Belgica en 1897-1898-1899. *Rapports Scientifiques. Botanique* 6: 1–129.
- Vinocur, A., and Maidana, N.I. 2010. Spatial and temporal variations in moss-inhabiting summer diatom communities from Potter Peninsula (King George Island, Antarctica). *Polar Biology* 33: 443–455. doi: 10.1007/s00300-009-0719-x
- Warnock, J.P., and Doran, P.T. 2013. Distribution of silicious-walled algae in Taylor Valley, Antarctica lakes. *International Journal of Geosciences* 4: 688–699. doi: 10.4236/ijg.2013.44064
- West, W., and West, G.S. 1911. Freshwater algae. British Antarctic Expedition (1907–1909) Science Report, Biology 1: 263–298.

- Whittaker, T.E., Hall, B.L., Hendy, C.H., and Spaulding, S.A. 2008. Holocene depositional environments and surface-level changes at Lake Fryxell, Antarctica. *The Holocene* 18: 775–786. doi: 10.1177/0959683608091797
- Zidarova, R., Levkov, Z. and Van de Vijver, B. 2014. Four new *Luticola* taxa (Bacillariophyta) from Maritime Antarctica. *Phytotaxa* 170: 155–168. doi: 10.11646/phytotaxa.170.3.2