

Boise State University

ScholarWorks

---

Geosciences Faculty Publications and  
Presentations

Department of Geosciences

---

2-2021

## Diatoms in Hyporheic Sediments Trace Organic Matter Retention and Processing in the McMurdo Dry Valleys, Antarctica

Anna J. Bergstrom  
*Boise State University*

---

### Publication Information

Heindel, Ruth C.; Darling, Josh P.; Singley, Joel G.; Bergstrom, Anna J.; McKnight, Diane M.; Lukkari, Braeden M.; . . . and Gooseff, Michael N. (2021). "Diatoms in Hyporheic Sediments Trace Organic Matter Retention and Processing in the McMurdo Dry Valleys, Antarctica". *JGR Biogeosciences*, 126(2), e2020JG006097-1 - e2020JG006097-17. <https://doi.org/10.1029/2020JG006097>

This document was originally published in *JGR Biogeosciences* by Wiley on behalf of the American Geophysical Union. Copyright restrictions may apply. <https://doi.org/10.1029/2020JG006097>

# JGR Biogeosciences

## RESEARCH ARTICLE

10.1029/2020JG006097

### Key Points:

- Diatoms from stream microbial mats were found in hyporheic zone, evidence of autochthonous organic matter transfer from channel to bed
- Biogenic silica correlated with loss-on-ignition, suggesting that diatoms indicate locations that promote organic matter retention
- *Nostoc* mats were the main source of hyporheic organic matter, confirming the role of atmospherically fixed N in stream nitrogen budgets

### Supporting Information:

- Supporting Information S1

### Correspondence to:

R. C. Heindel,  
[heindel1@kenyon.edu](mailto:heindel1@kenyon.edu)

### Citation:

Heindel, R. C., Darling, J. P., Singley, J. G., Bergstrom, A. J., McKnight, D. M., Lukkari, B. M., et al. (2021). Diatoms in hyporheic sediments trace organic matter retention and processing in the McMurdo Dry Valleys, Antarctica. *Journal of Geophysical Research: Biogeosciences*, 126, e2020JG006097. <https://doi.org/10.1029/2020JG006097>

Received 1 OCT 2020

Accepted 17 JAN 2021

### Author Contributions:

**Conceptualization:** Ruth C. Heindel, Josh P. Darling, Joel G. Singley, Anna J. Bergstrom, Michael N. Gooseff

**Data curation:** Ruth C. Heindel, Josh P. Darling

**Formal analysis:** Ruth C. Heindel, Josh P. Darling, Joel G. Singley

**Funding acquisition:** Diane M. McKnight, Michael N. Gooseff


**Methodology:** Ruth C. Heindel, Josh P. Darling, Joel G. Singley, Anna J. Bergstrom, Diane M. McKnight, Braeden M. Lukkari, Kathleen A. Welch

**Resources:** Diane M. McKnight, Michael N. Gooseff

**Supervision:** Diane M. McKnight, Michael N. Gooseff

© 2021. American Geophysical Union.  
All Rights Reserved.

## Diatoms in Hyporheic Sediments Trace Organic Matter Retention and Processing in the McMurdo Dry Valleys, Antarctica

Ruth C. Heindel<sup>1,2</sup> , Josh P. Darling<sup>1,3</sup> , Joel G. Singley<sup>1,3</sup> , Anna J. Bergstrom<sup>1,4</sup> , Diane M. McKnight<sup>1</sup> , Braeden M. Lukkari<sup>1</sup>, Kathleen A. Welch<sup>1</sup> , and Michael N. Gooseff<sup>1</sup> 

<sup>1</sup>Institute of Arctic and Alpine Research, University of Colorado Boulder, Boulder, CO, USA, <sup>2</sup>Environmental Studies Program, Kenyon College, Gambier, OH, USA, <sup>3</sup>Environmental Studies Program, University of Colorado Boulder, Boulder, CO, USA, <sup>4</sup>Department of Geosciences, Boise State University, Boise, ID, USA

**Abstract** In low-nutrient streams in cold and arid ecosystems, the spiraling of autochthonous particulate organic matter (POM) may provide important nutrient subsidies downstream. Because of its lability and the spatial heterogeneity of processing in hyporheic sediments, the downstream transport and fate of autochthonous POM can be difficult to trace. In Antarctic McMurdo Dry Valley (MDV) streams, any POM retained in the hyporheic zone is expected to be derived from surface microbial mats that contain diatoms with long-lasting silica frustules. We tested whether diatom frustules can be used to trace the retention of autochthonous POM in the hyporheic zone and whether certain geomorphic locations promote this process. The accumulation of diatom frustules in hyporheic sediments, measured as biogenic silica, was correlated with loss-on-ignition organic matter and sorbed ammonium, suggesting that diatoms can be used to identify locations where POM has been retained and processed over long timescales, regardless of whether the POM remains intact. In addition, by modeling the upstream sources of hyporheic diatom assemblages, we found that POM was predominantly derived from N-fixing microbial mats of the genus *Nostoc*. In terms of spatial variability, we conclude that the hyporheic sediments adjacent to the stream channel that are regularly inundated by daily flood pulses are where the most POM has been retained over long timescales. Autochthonous POM is retained in hyporheic zones of low-nutrient streams beyond the MDVs, and we suggest that biogenic silica and diatom composition can be used to identify locations where this transfer is most prevalent.

**Plain Language Summary** Streams play an important role in the global carbon cycle by processing organic matter, some of which comes from plants and microbes living within the stream itself. A fraction of this organic matter is rapidly processed (broken down) in subsurface sediments adjacent to and below the stream channel, which makes it a difficult process to observe directly. In this study, we considered if diatoms, single-celled algae with silica cell walls that are often found within larger algal mats, can indicate the processing of organic matter in subsurface sediments of a stream in the McMurdo Dry Valleys (MDVs), Antarctica. We show that diatoms can be used to identify locations where organic matter is processed in subsurface sediments, and to identify the source of the organic matter. In the MDVs, the processing of organic matter from within the stream itself provides important nutrients for downstream organisms. This recycling of organic matter within the stream likely occurs in other ecosystems, and our results suggest that diatoms may be a powerful tool to track this process.

## 1. Introduction

Streams actively regulate water quality and contribute to global biogeochemical cycling through the metabolic processing of mobilized organic carbon (Battin et al., 2009; Hall et al., 2016; Harvey & Gooseff, 2015). Allochthonous sources (i.e., from outside the stream channel, such as litterfall) are often thought to dominate inputs of particulate organic matter (POM) to headwater streams (Tank et al., 2010). However, high lability autochthonous POM (i.e., produced within the stream channel, such as periphyton) may also contribute to within-stream biogeochemical spiraling, supplying critical nutrient subsidies to downstream ecosystems, especially for oligotrophic streams in polar, alpine, and arid ecosystems (Dahm et al., 2003;

**Writing – original draft:** Ruth C. Heindel, Josh P. Darling, Joel G. Singley, Anna J. Bergstrom

**Writing – review & editing:** Ruth C. Heindel, Josh P. Darling, Joel G. Singley, Anna J. Bergstrom, Diane M. McKnight, Braeden M. Lukkari, Kathleen A. Welch, Michael N. Gooseff

Fellman et al., 2011; Fenoglio et al., 2015; Jones et al., 1995a). Directly studying the downstream fate of autochthonous POM can be challenging, not only because allochthonous and autochthonous sources may be difficult to differentiate but also because the processing of POM may occur in the hyporheic zone, the highly heterogeneous subsurface region where surface water exchanges with the porous streambed (Burrows et al., 2017; Findlay, 1995; Harvey & Gooseff, 2015).

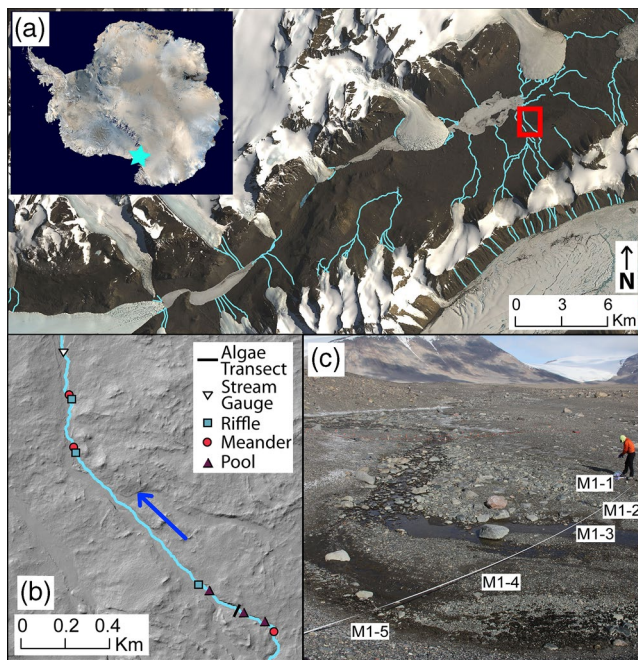
In order to be remineralized, POM must first be physically retained within hyporheic sediments (Tank et al., 2010), an exchange process regulated across multiple spatial and temporal scales (Harvey & Gooseff, 2015; Jones et al., 1995a, 1995b). Large-scale geomorphology of the stream channel such as meander bends and pool-riffle sequences, as well as intermediate-scale bedforms and surface roughness can result in complex spatial patterns of downwelling and lateral exchange that control where water and POM move into the hyporheic zone (Bergstrom et al., 2016; Boano et al., 2006; Cardenas et al., 2004; Findlay, 1995; Hendricks, 1993; Hill et al., 1998; Jones et al., 1995a; Tonina & Buffington, 2009). Fluctuating water levels also regulate the connectivity between surface water and the hyporheic zone, especially for intermittent and ephemeral streams in polar, alpine, and arid ecosystems that experience prolonged drought and episodic flooding (Burrows et al., 2017; Dahm et al., 2003; Fellman et al., 2011; Shumilova et al., 2019). Understanding if and where autochthonous POM is retained in the hyporheic zone is a first step toward tracing its downstream fate, but remains a challenge.

Once autochthonous POM is retained in hyporheic sediments, a similarly complex set of abiotic and biotic factors control the rate of POM decomposition, including the quality of the POM; the temperature, moisture, and redox conditions of the sediments; nutrient availability; and the heterotrophic microbial community composition (Burrows et al., 2017; Jones et al., 1995a; Tank et al., 2010). Following remineralization of POM, inorganic products such as ammonium can be retained within the hyporheic zone by sorption to sediments, further transformed by biogeochemical processes such as nitrification, or transported out of hyporheic sediments in upwelling zones (Jones et al., 1995b; Triska et al., 1994). For intermittent and ephemeral streams, cycles of rewetting following dry periods of preconditioning can lead to the episodic flushing of inorganic products of POM processing (Shumilova et al., 2019). Thus, discrete measurements of POM or inorganic remineralization products within hyporheic sediments may not be fully indicative of long-term rates of dynamic POM retention and processing.

The streams of the McMurdo Dry Valleys (MDVs) provide an ideal model ecosystem to study the hyporheic processing of autochthonous POM (Cullis et al., 2014; Gooseff et al., 2017; Howard-Williams et al., 1989; Kohler et al., 2018). In these glacially fed streams that cut across a landscape devoid of vascular plants, the only organic matter that can enter the hyporheic zone is sourced from the stream channels themselves. Perennial microbial mats, referred to in the MDV literature by their color, are the main source of POM. “Orange mats,” communities of mostly *Oscillatoria* spp. and *Phormidium* spp., line the center of the stream channel, while “black mats,” cyanobacterial communities of primarily *Nostoc* species, occupy the channel edges. Diatoms are an important and well-characterized component of both black and orange mat communities. At the margins of the stream channels, black mats coexist with up to eight species of moss (Ball & Virginia, 2014). The cohesive microbial mats do not appear to lose much organic material through leaching, and the concentration of dissolved organic matter (DOM) in the streams is typically well below  $1 \text{ mg C L}^{-1}$  (Aiken et al., 1996). Instead, POM is generated and transported downstream by daily flood pulses, driven by daily cycles in solar insolation and glacial melt (Conovitz et al., 1998), which scour the microbial mats (Cullis et al., 2014).

Multiple lines of evidence support the hypothesis that this mat-derived POM is retained and processed in the hyporheic zone, resulting in the release of remineralized nitrogen (N) that is later taken up by downstream microbial mats (Kohler et al., 2018; McKnight et al., 2004). With increasing distance downstream, the N isotope signature of orange mats, which are not known to fix atmospheric  $\text{N}_2$ , converges with that of the N-fixing black mats and atmospheric  $\text{N}_2$  (Kohler et al., 2018). This pattern suggests that the spiraling (remineralization, nitrification, and uptake) of *Nostoc*-derived (black mat) N dominates N availability in downstream reaches (Kohler et al., 2018; McKnight et al., 2004). Although this isotopic evidence provides strong support for the retention and remineralization of autochthonous POM in the hyporheic zone, these processes have thus far been inferred rather than studied directly.

We propose that silica diatom frustules are a novel tracer of POM that can indicate the presence of OM in the hyporheic zone and help overcome the challenges of observing POM processing in hyporheic



**Figure 1.** (a) Map of Taylor Valley showing the location of Von Guerard Stream in the red box, (b) close-up of the red box showing the locations of the nine hyporheic sediment transects and the streambed microbial mat transect used for the NMDS ordination and SourceTracker modeling, and (c) field photo showing the locations of the lateral sampling positions across the stream channel. NMDS, nonmetric multidimensional scaling.

sediments. Unlike other tracers of POM such as corn pollen, yeast, and bacteria that have been used previously to study POM retention elsewhere (Tank et al., 2010), diatom frustules are naturally occurring tracers that are sourced from within the stream, making them more suitable for tracing autochthonous POM. When microbial mats are scoured during daily flood pulses, labile mat material and the diatom frustules it contains are transported downstream and imported into the hyporheic sediments. However, in contrast to labile POM, diatom frustules do not break down rapidly because of their silica composition. Consequently, at a given location, the quantity of diatom frustules may be indicative of the quantity of POM retained and processed over timescales of years to centuries. Similarly, the community assemblage of hyporheic diatom frustules may reveal the source of the POM, because different mat types contain distinctive assemblages of widespread and endemic diatom taxa well-documented in the Antarctic Freshwater Diatoms database (Spaulding et al., 2020) of the McMurdo Dry Valleys Long Term Ecological Research (MCM LTER) project and other publications (Esposito et al., 2006, 2008; Stanish, 2011; Stanish et al., 2012). For other streams and rivers in North America, detailed descriptions of diatom floras are available via Diatoms of North America ([diatoms.org](http://diatoms.org)) and other databases (e.g., the Florida Everglades LTER).

In this study, we consider two main questions. First, is POM retained and processed in the hyporheic zone, and can diatom frustules be used to track these processes? If locations of POM retention in the hyporheic zone are stable over time, we would expect that diatom assemblage composition and frustule quantity are related to the more time-sensitive processes of POM degradation and remineralization. Second, are there geomorphic settings or lateral positions along the stream channel that promote the retention and processing of POM? Here, we predicted that depositional environ-

ments, such as stream margins, pools, and inner banks of meanders, would have higher rates of POM retention and processing in the long term.

To address these questions, we sampled hyporheic sediments across pools, riffles, and meander bends of Von Guerard Stream in Taylor Valley. First, we characterized the species composition of the diatom assemblages found within the hyporheic sediments and compared them to the known species composition of diatom communities associated with orange and black microbial mats. Second, we tested whether the quantity of diatom frustules, measured as percent biogenic silica, correlated with more time-sensitive geochemical indicators of POM retention and processing. At the most time-sensitive end of the spectrum, we measured rapidly degrading chlorophyll pigments. Next, loss-on-ignition (LOI) organic matter targets not only autochthonous POM imported into the hyporheic sediments, but also the heterotrophic bacterial communities that develop to consume POM. Finally, inorganic sorbed N, a product of POM remineralization, can remain bound to hyporheic sediments until cation exchange conditions change (Triska et al., 1994).

## 2. Methods

### 2.1. Site Description

The MDVs are located on the western edge of the Ross Sea and are the largest expanse of ice-free land on the Antarctic continent (Levy, 2012). The MDV landscape is composed of mountain glaciers, bare soils, incised stream channels, and perennially ice-covered closed basin lakes. The region is a polar desert, with valley floors receiving only 3–50 mm year<sup>−1</sup> of annual precipitation, all in the form of snow (Fountain et al., 2010). Taylor Valley, the location of this study, extends east from Taylor Glacier to the McMurdo Sound (Figure 1a). In the eastern half of the valley, the Fryxell Basin is home to 13 streams that flow into Lake Fryxell, a perennially ice-covered closed-basin lake (Wlostowski et al., 2016).



Streamflow is generated by glacial melt, which occurs only during the height of the austral summer, mid-December through mid-February (Wlostowski et al., 2016). Daily cycles in solar insolation drive glacier melt, resulting in dramatic daily pulses in stream discharge (10-fold increases in discharge are not uncommon during the warmest parts of the austral summer) that are responsible for scouring microbial mats and increasing POM concentrations in stream water (Cullis et al., 2014). Streams occupy overincised, stable channels that are cut down into glacial drift underlain by continuous permafrost. We focus specifically on Von Guerard Stream, one of the best-studied streams in Taylor Valley and the site of a concurrent study of hyporheic porewater. Von Guerard Stream extends 5.2 km from the Kukri Hills into Lake Fryxell (Figure 1), and as one of the longer streams in Taylor Valley, it has a relatively low median daily mean discharge ( $1.8 \text{ L s}^{-1}$ ) and a higher likelihood of having no flow during the typical flow season than short streams in Taylor Valley (Wlostowski et al., 2016).

## 2.2. Field Methods

During January 2019, we collected hyporheic sediments from a total of nine transects across three geomorphology types—pools, meanders, and riffles—along Von Guerard Stream in Taylor Valley (Figure 1). Each transect was composed of five sampling sites at different lateral positions across the stream channel: two sampling sites were located at the margins of the visible wetted zone (lateral positions 1 and 5, referred to as “edge”), one sampling site was directly under the thalweg (lateral position 3, “thalweg”), and two sampling sites were located halfway between the wetted margin and the thalweg (lateral positions 2 and 4, “intermediate”). Transects ranged from 6.6 to 13.6 m in total length. At each sampling site, we removed the surface sediment and mat material in order to sample only the underlying hyporheic sediments. With a clean scoop for each sample, we collected bulk sediment down to 10 cm into Whirl-Pak® sampling bags. These samples were used for all laboratory analyses other than diatom assemblage composition. To characterize the hyporheic diatom assemblages, we collected a separate sample in a plastic scintillation vial that was preserved in formalin directly after sample collection. Bulk samples were frozen immediately after sample collection and remained frozen until laboratory analyses.

At the time of sampling on January 10, 2019, the majority of the season’s streamflow had already occurred. The largest daily flood pulses of the 2018–2019 season took place in late December 2018; the final large ( $>15 \text{ L s}^{-1}$ ) flood pulse of the season occurred on December 22, 2018 and reached a discharge of  $42 \text{ L s}^{-1}$ . At the time of sampling, discharge ranged from  $0.2$  to  $0.5 \text{ L s}^{-1}$ , with a daily peak of only  $1.4 \text{ L s}^{-1}$  (Gooseff & Mcknight, 2021).

## 2.3. Diatom Assemblages

### 2.3.1. Laboratory Methods

We characterized diatom assemblages for six of the nine transects (30 of 45 samples) by counting a total of 300 diatom valves from each preserved diatom sample. Counting and identifying diatoms is labor-intensive; this subset allowed us to characterize two transects (the farthest upstream and the farthest downstream) of each geomorphology type. We processed the diatom samples using standard techniques (Blanco et al., 2008). A subset of sediment was first transferred to 50-ml centrifuge tubes. We then cleaned samples of organic content by digesting with hydrogen peroxide (30 ml of 30%  $\text{H}_2\text{O}_2$ ) for 48 h at  $100^\circ\text{C}$ . After digestions were complete, samples were repeatedly rinsed with distilled water until a neutral pH was reached. We isolated diatoms from sand grains and other mineral aggregates through repeated resuspension and centrifugation to carefully retain the diatoms in the supernatant. Aliquots of supernatant were dried on coverslips and mounted to glass microscope slides using a highly refractive adhesive (Zrax, W. P. Dailey, Philadelphia, USA). We counted diatoms at  $\times 1,250$  magnification on an Olympus BX50 DIC microscope and identified taxa using descriptions listed in the Antarctic Freshwater Diatoms database (Spaulding et al., 2020). Fragmented diatom frustules were identified to the highest taxon-level possible (mostly genus level) and we calculated the ratio between fragmented frustules to the total number of intact diatoms counted for each sample. For statistical analysis, we removed species that did not exceed 3% relative abundance in any sample. All relative abundance composition data was standardized to 300 diatom valves per sample.

### 2.3.2. Statistical Methods

We compared hyporheic diatom assemblages with previously described streambed microbial mat communities using ordination and modeling techniques. For the microbial mat communities, we used data from 10 orange mat and 10 black mat samples collected from Von Guerard Stream “lower” sampling transect (Figure 1b) between 1994 and 2014 as part of the MCM LTER. Diatom community composition data from MCM LTER monitoring samples were downloaded from the Antarctic Freshwater Diatoms database. We chose to use samples from the Von Guerard Stream “lower” transect because it is located near and upstream of most of the hyporheic sediment transects (Figure 1b), and mats at this site are a potential upstream source of diatoms entrained into hyporheic sediments. We selected an equal number (10) of both orange and black mat samples from comparable collection dates representing a timespan from 1994 to 2014 and collected over a range of total annual streamflow (selected samples are listed in Table S1). The MCM LTER diatom database uses taxon codes assigned to species morphologies to promote taxonomic consistency through the record and to allow for comparison to other records. These streambed microbial mat samples were processed and counted with the methods described above.

To visualize compositional relationships between the hyporheic diatom assemblages and streambed mat communities, we used a nonmetric multidimensional scaling (NMDS) ordination with “bray” distance dissimilarity. The ordination was followed by non-parametric methods for multivariate analysis of variance (PERMANOVA), with significance set at  $\alpha = 0.05$  (Andersen, 2001). We used the R package *vegan* for the ordination analysis (Oksanen et al., 2019).

We modeled hyporheic diatom assemblages as a mixture of upstream sources with a Bayesian community-wide approach using SourceTracker version 0.9.1 (Knights et al., 2011). SourceTracker models sink assemblages as a mixture of communities from potential source environments with unknown mixing proportions. The model uses Gibbs sampling to estimate the mixing proportions from source assemblages (Knights et al., 2011). SourceTracker is initiated with a set of prior parameters ( $\alpha$ ,  $\alpha_2$ , and  $\beta$ ), which smooth the distribution for low-coverage samples and allow for unknown sources when sink samples are unlike known source communities (Knights et al., 2011). To train the model and optimize the prior parameters, we used the 20 streambed microbial mat samples described above as a training data set (Table S1). The prior parameters were optimized on this training data set by iteratively running the model with different parameter values and comparing the model predictions to known mixing proportions for the source samples (Figure S1). Using these optimized parameters ( $\alpha = 0.001$ ,  $\alpha_2 = 0.1$ , and  $\beta = 0.01$ ), we used the model to estimate the proportions of the hyporheic assemblages derived from upstream orange mat, black mat, and unknown communities.

## 2.4. Geochemical Indicators

### 2.4.1. Laboratory Methods

For all hyporheic sediment samples ( $N = 45$ ), we measured multiple geochemical indicators of POM retention and processing (chlorophyll pigments, organic matter, sorbed inorganic N, UV absorbance, and biogenic silica), described here in order from most time-sensitive to most stable.

To quantify chlorophyll *a* and its degraded pheopigments, we used an acetone extraction followed by spectroscopy. Approximately 30 g of hyporheic sediment was extracted in 20 ml 90% buffered acetone for 24 h. The suspended material was then centrifuged for 10 min at 1,500 rpm and the extracted supernatant was decanted into glass scintillation vials. In order to normalize pigment values to sediment dry weight, the remaining sediment portion was dried at 55°C for 72 h and weighed; we report fluorescence values as concentrations of chlorophyll *a* and pheophytin by dry weight. We measured the chlorophyll fluorescence of the extracted pigment spectroscopically using a FluoroMax F3 fluorometer (HORIBA Jobin Yvon) following well-established methods (Holm-Hansen et al., 1965; Wetzel & Likens, 2013). We measured pheophytin concentrations on the same samples used for chlorophyll by taking the difference in fluorescence after acidification (100  $\mu$ l 0.1-M hydrochloric acid). In our statistical analysis, we use the combined chlorophyll *a* and pheophytin value because we are interested in longer timescales and both pigments are indicative of POM retention within the hyporheic zone.

To quantify the amount of organic matter in the hyporheic sediments, we dried and combusted sample subsets. Approximately 20 g of wet, homogenized sediment was subsampled for each site, weighed and then dried at 105°C for 24 h. Samples were reweighed to determine dry weight and gravimetric moisture content. Dried samples were then combusted in a muffle furnace at 450°C for 4 h and reweighed to calculate LOI relative to dry weight.

We measured inorganic N adsorbed to the sediments using a 2-M KCl extraction. Approximately 20 g of wet, homogenized sediment from each site was weighed into sterile HDPE sample cups. We added 80 ml of 2-M KCl, inverted the cups three times and placed them on an elliptical shaker table at 400 rpm for 1 h. Samples were removed from the shaker table, allowed to settle for 1 h, and filtered through Whatman Qualitative Grade 1 filter paper. Filtered extracts were stored frozen until the time of analysis. Both extractable N as ammonium ( $\text{NH}_4^+$ -N) and as combined nitrate and nitrite ( $\text{NO}_2^-$ -N +  $\text{NO}_3^-$ -N, referred to as  $\text{NO}_3^-$ -N hereafter) were measured using a Lachat Quickchem Flow Injection Analysis System (Hach) according to standard protocols 4500-NH<sub>3</sub> (phenolate FIA) and 4500-NO<sub>3</sub> (cadmium reduction FIA). Concentrations for each N species were normalized to sample dry weights, which were estimated using gravimetric moisture content determined during the LOI protocol. The minimum detection limits were 0.005-mg  $\text{NH}_4^+$ -N L<sup>-1</sup> and 0.004-mg  $\text{NO}_3^-$ -N L<sup>-1</sup>.

The KCl extraction used to measure inorganic N is also expected to desorb organic matter from the sediment (Gabor et al., 2015). To evaluate the potential relationship between inorganic N and soluble organic matter, we also determined the UV absorbance spectra of the KCl extracts using an Agilent 8453 UV-visible spectrophotometer. The humic fraction of the soluble organic matter is expected to have an absorbance peak at 254 nm associated with the absorbance by aromatic ring structures (Gabor et al., 2015).

We measured the percent biogenic silica (diatom quantity) of the hyporheic sediments using a hot NaOH extraction, following the standard operating procedure from the National Lacustrine Core Facility (Chan, 2011). To account for the low levels of biogenic silica in our samples, we used 300 mg of oven-dried sediment for the extractions (Spaulding et al., 1997). To digest the samples, we added 38 ml of 0.5-M NaOH to the samples and immediately placed them in an 85°C water bath. We subsampled aliquots at 60, 90, 120, and 200 min to account for the slow dissolution of clay minerals (DeMaster, 1981). Aliquots were reacted with color reagents to form molybdate blue and measured spectroscopically using an Agilent 8453 UV-visible spectrophotometer. To arrive at the percent biogenic silica for each sample, we calculated the linear equation for the 90, 120, and 200-min aliquots for each sample and assumed the intercept to be the percent biogenic silica with no additional silica from clay dissolution. We disregarded the first time point (60 min) because it consistently did not follow the linear relationship of the subsequent three time points. We believe this was due to an incomplete dissolution of the biogenic silica at the first time point, potentially due to the presence of intact and viable diatom frustules in our samples.

#### 2.4.2. Statistical Methods

To understand the spatial controls on POM retention and processing in the hyporheic sediments, and to assess the potential for using percent biogenic silica as a POM tracer, we took an information-theoretic model comparison approach. For the more time-sensitive indicators of chlorophyll pigments (the sum of chlorophyll *a* and pheophytin), percent LOI, and  $\text{NH}_4^+$ -N, we generated a list of candidate models that included all plausible combinations of geomorphology type, absolute distance from the thalweg, percent biogenic silica, and their interactions as fixed effects. All models included transect as a random effect. Prior to running the mixed models, we identified and removed any outliers that were more than 2.5 times the interquartile range beyond the first or third quartile. This resulted in the removal of two outliers from the chlorophyll pigments data set and two outliers from the  $\text{NH}_4^+$ -N data set ( $N = 43$  for these data sets).

Using the second-order Akaike's information criteria (AICc: [Hurvich & Tsai, 1989], we ranked candidate models and here present the three top-ranked models (R package *AICcmodavg*: Mazerolle, 2020). Models are generally considered plausible when the  $\Delta\text{AICc} < 2$  relative to the top-ranked model. For each top-ranked model, we used the R package *MuMIn* to calculate an  $R^2$  for the entire model, including both fixed and random effects (Bartón, 2020).

**Table 1**

List of 16 Dominant Species That Influence the Compositional Shifts Between Assemblages With Summary Information on Species Authority, Size Range, and Biogeographic Distribution

Species name	Authority <sup>a</sup>	Species code	Length (μm)	Width (μm)	Distribution
<i>Achnanthes taylorensis</i>	Kellogg et al. (1980)	Atay	25–38	7–10	Antarctica
<i>Fistulifera pelliculosa</i>	(Kützing) Lange-Bertalot (1997)	Fpel	7.5–10	4–5.5	Widespread
<i>Hantzschia abundans</i>	Lange-Bertalot (1993)	Habu	49–94	7–9.5	Widespread
<i>Hantzschia amphioxys</i>	(Ehrenberg) Grunow (1880)	Hamp	21–50	4.5–7	Widespread
<i>Hantzschia amphioxys f. muelleria</i>	(Ehrenberg) Ko-Bayashi (1965)	Hmue	23–44	5–7	Antarctica
<i>Luticola austroatlantica</i>	Van de Vijver et al. (2008)	Laus	6.4–30	4.4–8.2	Antarctica
<i>Luticola muticopsis</i>	(Heurck) Mann (1990)	Lcop	12–37.1	5–9	Antarctica
<i>Luticola dolia</i>	Spaulding and Esposito (2008)	Ldol	11.3–25.1	5.4–7.7	South Victorialand
<i>Luticola mcknightiae</i>	Kohler and Kopalová (2015)	Lmck	12–23	7–10	Antarctica
<i>Luticola mutica</i>	(Kützing) Mann (1990)	Lmut	7–29	5.5–8	Widespread
<i>Mayamaea atomus</i>	(Kützing) Lange-Bertalot (1997)	Maya	6.5–10	1.5–5.5	Widespread
<i>Mayamaea atomus</i> var. 1	Kützing (1844)	Mayv	12–14	5–6	South Victorialand
<i>Nitzschia australocommutata</i>	Hamsher et al. (2016)	Naus	37.7–58.9	6–6.3	South Victorialand
<i>Navicula seibigiana</i>	Lange-Bertalot (1993)	Nsei	13–35	4.5–7.5	Widespread
<i>Navicula shackeltoni</i>	West and West (1911)	Nsha	19–32	4–5	South Victorialand
<i>Stauroneis latistauros</i>	Van de Vijver and Lange-Bertalot (2004)	Slat	25–53	6–9.7	Widespread

Note. Species codes are referenced in Figure 2

<sup>a</sup>For references and more information about species authorities, please visit the Antarctic Diatom Database (Spaulding et al., 2020).

### 3. Results

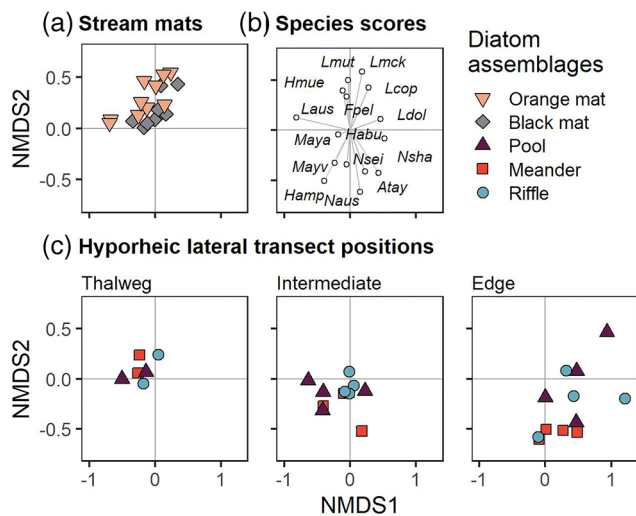
#### 3.1. Diatom Assemblages

Diatom species such as *Luticola muticopsis*, *Hantzschia amphioxys f. muelleria*, and *Luticola austroatlantica* (Tables 1 and S2), known to be abundant in surface microbial mats (Esposito et al., 2006), were also abundant in hyporheic assemblages. Species richness values were also similar between hyporheic assemblages (13–31 species per sample) and surface microbial mat communities (16–33 species per sample). Of the 16 dominant species, 9 were Antarctic endemics (Table 1).

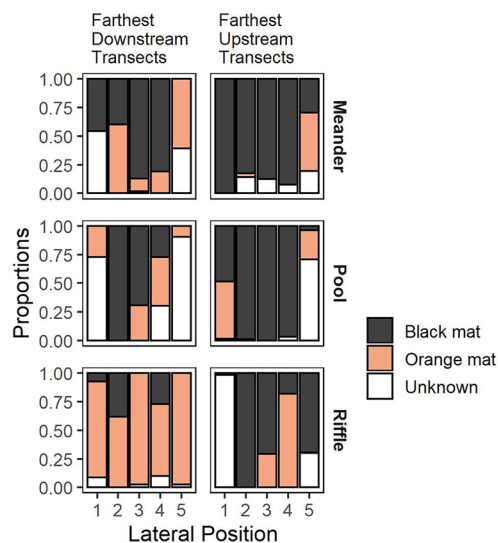
There were significant differences in diatom composition among the sample types. First, orange and black mat diatom communities were significantly distinct from one another (PERMANOVA,  $F = 2.974$ ,  $p = 0.03$ ). Second, there were significant differences in the composition between hyporheic and mat assemblages and across lateral stream position (Figure 2). Comparing hyporheic assemblages to surface mat communities, hyporheic assemblages from under the thalweg (lateral position 3) were not significantly different from the mat communities, with abundant *L. austroatlantica*, *Luticola permuticopsis*, *Stauroneis latistauros* (Table 1), and other common surface microbial mat species. On the other hand, the assemblages from the edges (lateral positions 1 and 5) of meanders, riffles and pools were significantly different from the orange and black mat communities ( $F = 3.597$ ,  $p = 0.01$ ), and contained more endemic taxa, such as *Nitzschia australocommutata*, *Mayamaea atomus* var #1, and *Luticola dolia* (Table 1), that are typically not as abundant in black and orange mat communities. Comparing among hyporheic lateral positions revealed a similar pattern. There was no significant difference between thalweg and intermediate (lateral positions 2 and 4) assemblages, but the edge assemblages were statistically different from thalweg ( $F = 3.49$ ,  $p = 0.01$ ) and intermediate ( $F = 4.143$ ,  $p = 0.01$ ) positions.

Similar to the NMDS and PERMANOVA results, the SourceTracker modeling showed distinct differences in the sources of hyporheic diatoms across the lateral positions (Figure 3). Hyporheic diatoms under the thalweg (lateral position 3) were primarily sourced from orange and black mats, whereas edge assemblages





**Figure 2.** Nonmetric multidimensional scaling (NMDS) ordination of surface and hyporheic diatom assemblages (3D stress = 0.13, PERMANOVA  $F = 3.3275$ ,  $p = 0.001$ ), separated into multiple panels for improved visibility. (a) Diatom assemblages from surface orange (inverse triangle) and black (diamond) stream microbial mats, (b) species scores indicating the correspondence of select species with the primary axes (see Table 1 for species code explanations), and (c) hyporheic diatom assemblages from under the thalweg, intermediate, and edge lateral positions across pool (purple triangle), meander (red square), and riffle (blue circle) transects. PERMANOVA, parametric methods for multivariate analysis of variance.



**Figure 3.** Estimated proportion of hyporheic diatom assemblages sourced from upstream orange and black microbial mat communities at the farthest upstream and downstream transects for each geomorphic unit. The estimated mixing proportion of hyporheic diatom assemblages was modeled using SourceTracker version 0.9.1 (Knights et al., 2011).

(lateral positions 1 and 5) had higher variability in the proportion of unknown sources. Black mats were the dominant source of diatoms across geomorphology type and lateral position, except at for the downstream riffle site where orange mats were consistently dominant for all lateral positions (Figure 3). Unknown sources were predicted for assemblages that lacked a “core” set of taxa and were unlike known orange and black mat sources (Knights et al., 2011). Assemblages that had a high proportion of unknown sources had a greater abundance of species of genera not typically dominant in stream mats (e.g., *Achnanthes*, *Mayamaea*, *Navicula*, *Nitzschia*, and *Pinnularia*) as well as both freshwater and marine diatom fragments.

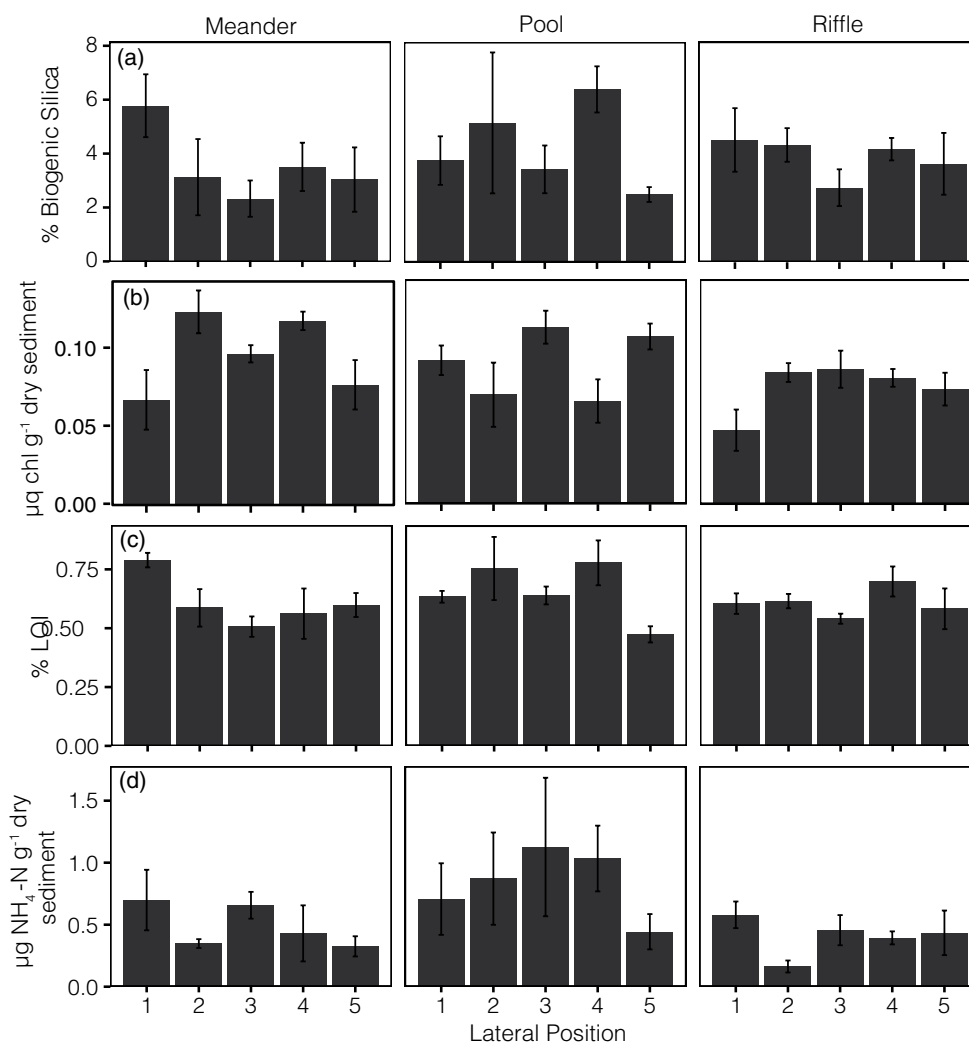
### 3.2. Indicators of POM Processing

Biogenic silica, which we use here as a proxy for the quantity of diatom frustules in hyporheic sediments, ranged from 1.1% to 10.4% dry sediment by mass. This range is similar to the 0.05%–5% biogenic silica previously measured in sediments from Lake Hoare, one of the perennial ice-covered lakes in Taylor Valley (Spaulding et al., 1997). In the hyporheic sediments measured here, the highest values of biogenic silica were at lateral position 1 (the inner bank) of meanders ( $5.8 \pm 1.2\%$ , mean  $\pm$  standard error,  $n = 3$ ) and lateral positions 2 and 4 of pools ( $5.8 \pm 1.3\%$ ,  $n = 6$ ), whereas the lowest values were under the thalweg (lateral position 3) for all geomorphology types ( $2.8 \pm 0.4$ ,  $n = 9$ ) (Figure 4).

Total chlorophyll pigment (chlorophyll  $a$  + pheophytin) concentrations were variable, ranging from 0.029 to 0.313  $\mu\text{g g}^{-1}$  dry sediment, and were not well explained by spatial variables (absolute distance from the thalweg and geomorphology type) or percent biogenic silica. Chlorophyll  $a$  concentrations ranged from 0.011 to 0.099  $\mu\text{g g}^{-1}$  dry sediment, while pheophytin concentrations ranged from below detection to 0.298  $\mu\text{g g}^{-1}$  dry sediment. The ratio of chlorophyll  $a$  to pheophytin mostly fell within the range of 0.5–5, with an average of 1.9 after removing two outliers  $> 50$ . The top-ranked mixed model identified geomorphology and distance from the thalweg as main effects on chlorophyll pigment concentration, but the model  $R^2$  was only 0.23 (Tables 2 and 3). Distance from the thalweg had a slight negative effect on chlorophyll pigment concentrations, with the highest concentrations directly under the thalweg at lateral position 3. Meanders and pools had higher and more variable concentrations compared to riffles (meanders:  $0.094 \pm 0.008 \mu\text{g g}^{-1}$  dry sediment, pools:  $0.088 \pm 0.007 \mu\text{g g}^{-1}$  dry sediment, riffles:  $0.074 \pm 0.005 \mu\text{g g}^{-1}$  dry sediment, mean  $\pm$  standard error).

Organic matter, measured as LOI, ranged from 0.36% to 0.95% dry sediment and was positively correlated with percent biogenic silica. The top-ranked model included only biogenic silica as a fixed effect, with a model  $R^2$  of 0.62 (Tables 2 and 3). There were no other plausible models; the second and third-ranked models both had  $\Delta\text{AICc} > 2$ . Although not significant, there were some spatial patterns in LOI. Similar to the results for percent biogenic silica, the highest values of LOI were found at the inner banks of meanders (lateral position 1) and at lateral positions 2 and 4 of pools (Figure 4).

All samples had detectable levels of extractable  $\text{NH}_4^+\text{-N}$ , which ranged from 0.1 to 3.7  $\mu\text{g N g}^{-1}$  dry sediment. In contrast,  $\text{NO}_3^-\text{-N}$  and  $\text{NO}_2^-\text{-N}$  were below detection for all but three samples and were not analyzed



**Figure 4.** Hyporheic sediment characteristics for transects across meanders, pools, and riffles. (a) Percent biogenic silica, (b) chlorophyll pigments (chlorophyll *a* + pheophytin), (c) percent loss-on-ignition, and (d) sorbed ammonium. Error bars =  $\pm 1$  standard error.

further. Geomorphology, distance from the thalweg, and biogenic silica were all identified as main effects on  $\text{NH}_4^+\text{-N}$  by the top-ranked model, which had a model  $R^2$  of 0.47 (Tables 2 and 3). Similar to our findings for chlorophyll pigments, distance from the thalweg had a slight negative effect on  $\text{NH}_4^+\text{-N}$ . Pools had the highest concentrations of  $\text{NH}_4^+\text{-N}$ , meanders were intermediate, and riffles had the lowest concentrations (pools:  $0.82 \pm 0.13 \mu\text{g N g}^{-1}$  dry sediment, meanders:  $0.50 \pm 0.07 \mu\text{g N g}^{-1}$  dry sediment, riffles:  $0.41 \pm 0.06 \mu\text{g N g}^{-1}$  dry sediment, mean  $\pm$  standard error).

Just less than half of the samples (20 of 45) had detectable UV absorbance at 254 nm, an indicator of extractable humic material (Figure S2). The 11 samples where UV absorbance was detected at higher concentrations ( $>0.1$  at 254 nm) were distributed across all transects and lateral positions. The absorbance spectra of these higher concentration samples were typical for humic material, with decreasing absorbance with increasing wavelength (Figure S3). There was no significant correlation with sorbed ammonium in the KCl extracts or with the other measured parameters, and the UV absorbance was not included in further statistical analysis.

Among the three more time-sensitive indicators of POM retention and processing (chlorophyll pigments, LOI, and  $\text{NH}_4^+\text{-N}$ ), there was a significant positive correlation between LOI and  $\text{NH}_4^+\text{-N}$  after removing the

**Table 2**  
The Three Top-Ranked Models for Each Variable Modeled

Model rank	Predictor variables	No. of parameters	AICc	$\Delta$ AICc	AICc model weight	Log-likelihood
Chlorophyll pigments (chlorophyll + pheophytin)						
1	Geomorph + distance	6	−186.91	0.00	0.30	100.62
2	Distance	4	−186.62	0.28	0.26	97.84
3	Distance + biogenic silica	5	−184.55	2.36	0.09	98.08
Loss-on-ignition						
1	Biogenic silica	4	−85.96	0.00	0.67	47.48
2	Distance + biogenic silica	5	−83.43	2.53	0.19	47.48
3	Geomorph + biogenic silica	6	−81.54	4.42	0.07	47.88
Sorbed ammonium						
1	Geomorph + distance + biogenic silica	7	29.49	0.00	0.35	−6.15
2	Biogenic Silica + geomorph + biogenic silica:geomorph	8	30.05	0.55	0.27	−4.91
3	Biogenic silica + geomorph	6	30.43	0.94	0.22	−8.05

AICc, Akaike's information criteria.

two outliers identified in the  $\text{NH}_4^+$ -N data set ( $R^2 = 0.29$ ,  $p = 0.0002$ ). There were no correlations between chlorophyll pigments and either LOI or  $\text{NH}_4^+$ -N.

### 3.3. Spatial Patterns in POM Retention and Processing

When combined, the hyporheic sediment chemistry and diatom assemblages indicate lateral positions across the stream channel that promote the retention and processing of POM (Figure 5). In hyporheic sediments beneath the thalweg (lateral position 3), diatom assemblage compositions suggest that POM is sourced entirely from black and orange mats. However, this is also the location of the lowest percent biogenic silica and LOI, suggesting that sediments beneath the thalweg are not stable locations of autochthonous POM

retention and processing over time. In hyporheic sediments farthest from the thalweg beneath the wetted margins (lateral positions 1 and 5, “edge”), diatom assemblages suggest sources other than black and orange mats. The moderate values of biogenic silica and LOI thus likely do not represent processing of stream-derived POM, but instead indicate either legacy material from ancient lake sediments or moss-derived material (Berger et al., 2013). At the intermediate sites (lateral positions 2 and 4), both diatom quantity and composition suggest that there is processing of autochthonous POM: diatom assemblages are similar to both orange and black mat communities and percent biogenic silica is highest on average compared to the other lateral positions (Figure 5).

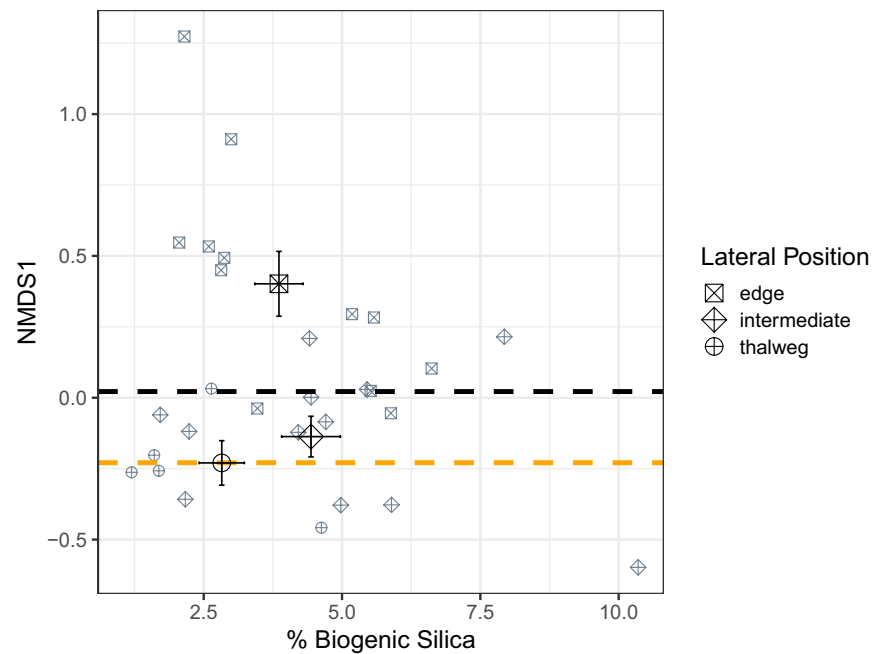
## 4. Discussion

### 4.1. Diatom Community Assemblage as Indicator of POM Source

The results outlined above provide direct evidence of the delivery of autochthonous POM into the hyporheic sediments of Von Guerard Stream. The presence of surface microbial mat diatoms such as *L. muticopsis*, *Hantzschia amphioxys* f. *muelleria*, and *L. austroatlantica* in the hyporheic zone allows us to use biogenic silica as a tracer of POM quantity and diatom assemblage as a tracer of POM source. This study is one of the first to investigate the composition of diatom assemblages in the hyporheic zone (Hendricks, 1993; Kloep & Röske, 2004), and is the first we

**Table 3**  
Statistics and Parameter Estimates for the Top-Ranked Model for Each Variable

Parameter	Estimate	Std error	p-Value
Chlorophyll pigments (model $R^2 = 0.23$ )			
Intercept	0.106	0.008	0
Geomorph (pool)	−0.006	0.009	0.5099
Geomorph (riffle)	−0.021	0.009	0.0303
Distance	−0.004	0.002	0.0159
Loss-on-ignition (model $R^2 = 0.62$ )			
Intercept	0.421	0.029	0
Biogenic silica	0.052	0.007	0
Sorbed ammonium (model $R^2 = 0.47$ )			
Intercept	0.276	0.123	0.0315
Biogenic silica	0.097	0.024	0.0003
Distance	−0.037	0.02	0.0699
Geomorph (pool)	0.228	0.114	0.0931
Geomorph (riffle)	−0.142	0.111	0.2483



**Figure 5.** Differences in hyporheic diatom assemblage (NMDS1 as per Figure 3) and diatom quantity (% biogenic silica) by lateral position across the stream channel. Dashed lines show the NMDS1 scores of orange mat assemblages (orange line) and black mat assemblages (black line). Gray points show individual hyporheic samples and the black points show the mean for each lateral position. Error bars =  $\pm 1$  standard error. NMDS, nonmetric multidimensional scaling.

are aware of that uses biogenic silica and diatom assemblage to trace POM retention and processing in hyporheic sediments.

The degree of similarity between microbial mat diatom communities and hyporheic assemblages differed by lateral position across the stream channel. Diatom assemblages in hyporheic sediments from beneath the thalweg were not statistically distinct from surface microbial mat communities, but assemblages in hyporheic sediments at the wetted margin (2–10 m from the stream channel center) were statistically different. The diatoms responsible for the compositional shift in the assemblages of edge samples (lateral positions 1 and 5) are not as common in the orange and black mat communities (Figure 2). For instance, edge assemblages had higher abundances of various *Mayamaea* taxa and in some cases more *Navicula shakletoni*, which may be relicts of past periods of lake level change in the Fryxell Basin (Berger et al., 2013). The high number of frustule fragments found in these edge samples supports the idea that the edge diatoms may be thousands of years old. In addition to these ancient lake diatoms, some taxa common in edge samples, such as *Achnanthes taylorensis*, *Navicula seibigiana*, and *Nitzschia australocommutata*, may be associated with extant moss communities that are present along the stream margins beyond the black mat habitat (Ball & Virginia, 2014). Regardless, it is clear that the diatom assemblages at the wetted margin are not sourced primarily from within the stream channel, and thus their presence does not indicate the processing of autochthonous POM within the stream corridor.

The results from the SourceTracker modeling indicate that the diatoms within the hyporheic zone were sourced from both orange and black mat types, but that black mat sources dominated the majority of samples from lateral positions 2–4 (i.e., thalweg and intermediate positions; Figure 3). This result agrees with the previous finding that the N isotopic signature of POM in streamwater is much closer to that of black mats than orange mats (Kohler et al., 2018). The tendency of black mats to slough off during daily flood pulses may be due to the rougher morphology compared to the smooth orange mats and the location of black mats on the margin of the stream channel, where they experience fluctuating water levels and frequent desiccation. Because black mats are N-fixers, the predominance of black mat POM suggests that N availability may be driven more by within-stream N fixation and subsequent transformations, rather than

N derived from atmospheric deposition onto glacier surfaces (Witherow et al., 2006). Because benthic algae are N-limited in some MDV streams (Gooseff et al., 2004), the spiraling of autochthonous POM and N from N-fixing mats likely serves as a major control on the growth of non-N-fixing mats. Autochthonous POM and DOM generated by *Nostoc*, the globally distributed N-fixing genus of MDV black mats (Dodds et al., 1995), likely play an important role in N budgets and in-stream primary production in many other low-nutrient freshwater ecosystems.

#### 4.2. Biogenic Silica as Indicator of Organic Matter Processing

The diatom community assemblages discussed above suggest that the main source of biogenic silica in the MDV hyporheic sediments is diatom frustules sourced from surface microbial mats. Although silicate chemical weathering rates are relatively high in the MDVs due to the rapid flushing from continuous hyporheic exchange (Gooseff et al., 2002; Maurice et al., 2002; Wlostowski et al., 2018), a silica isotope study from the adjacent Crescent Stream determined that diatom dissolution plays a minor role in contributing to the silicate weathering rate (Hatton et al., 2020; Hirst et al., 2020). Similarly, in a lake sediment core from Lake Hoare in Taylor Valley, there was little microscopic evidence of the dissolution of diatom frustules (Spaulding et al., 1997). This evidence suggests that diatom frustules are stable in hyporheic sediments on timescales of decades to centuries, and thus can be used as long-term indicators of POM retention and processing.

The detection of the much more time-sensitive chlorophyll *a* indicates that microbial mat material is regularly entrained in the hyporheic zone (Figure 4). The chlorophyll *a* concentrations reported here ( $0.011\text{--}0.099\text{ }\mu\text{g g}^{-1}$  dry sediment) are similar to the lower end of concentrations reported for dry soils (Simmons et al., 2009), and are much lower than concentrations reported for surface microbial mats, which can extend up to  $50\text{--}100\text{ }\mu\text{g g}^{-1}$  dry sediment (Geyer et al., 2013; Power et al., 2020). The low values that we measured are likely due to the fact that chlorophyll pigments degrade during cellular senescence after POM enters the hyporheic zone (Louda et al., 1998). Contrary to our prediction, biogenic silica did not predict total chlorophyll pigment concentration (chlorophyll *a* plus the degradation product pheophytin, Table 2). For chlorophyll pigments, the low  $R^2$  of the top-ranked model suggests that we do not fully understand controls on the spatial variability of these rapidly degrading pigments in hyporheic sediments, which may be related to the type of microbial mat imported into the hyporheic sediments, the rate of pigment decay, and the ability of sediments to retain chlorophyll pigments (Hodgson et al., 2004).

Biogenic silica was a very strong predictor of LOI organic matter, which ranged from 0.36% to 0.95% of dry sediment (Table 2). These values of organic matter are more than an order of magnitude greater than total organic carbon measurements from the surrounding dry soils in the Fryxell Basin, which ranges from 0.068% to 0.015% (Burkins et al., 2001). Unlike measurements of chlorophyll concentrations that target only labile microbial mat material, measurements of total organic matter target both mat-derived POM and the heterotrophic bacterial communities that develop to consume and process POM, and so are not as time-sensitive. Invertebrate communities of nematodes, tardigrades, and rotifers could also influence LOI organic matter. However, the number of invertebrate grazers in microbial mats is low and is even lower in underlying sediment, ranging between  $24.85 \pm 6.22$  and  $45.66 \pm 17.68$  organisms per gram of sediment over 2 years of sampling (Andriuzzi et al., 2018), suggesting that our LOI results have not been strongly influenced by grazing. The strong correlation between biogenic silica and LOI suggests that there are stable locations of POM retention in the hyporheic zone where heterotrophic bacterial communities are well-established.

Biogenic silica was also a significant predictor of sorbed ammonium concentrations (Table 2), a longer-term indicator of POM processing. The masses of sorbed ammonium we found are comparable to or slightly higher than prior studies of MDV stream sediment, although those studies also detected nitrate concentrations (Barrett et al., 2002; Zeglin et al., 2011). As the first inorganic N product of OM remineralization, the presence of ammonium is a direct sign that this processing has occurred within the hyporheic sediments. In addition to biogenic silica, geomorphology type and distance from the thalweg were also significant factors in the top-ranked ammonium model (Table 2), with more sorbed ammonium in pools and in the center of stream channels (Figure 4). The depositional environments of pools may retain more clay minerals and fine-grained sediments (Lisle & Hilton, 1999), leading to a higher cation exchange capacity and ability to sorb ammonium than coarser sediments (Triska et al., 1994). In MDV streams, pools are shallow and



frequently located at the head of riffles, and are therefore likely to be zones of deposition (Hill et al., 1998; Valett et al., 1994). Across other stream types, although the specific channel morphology and flow regime will determine the exact location of depositional environments, the deposition of fine sediment remains important for the retention and release of nutrients within the stream ecosystem (Cushing et al., 1993; Drummond et al., 2014, 2017; Newbold et al., 2005).

The presence of ammonium sorbed to MDV hyporheic sediments contrasts with results of dissolved fractions of inorganic N species from a concurrent study of hyporheic porewater in Von Guerard Stream. In the porewater samples, dissolved ammonium was almost always below detection, suggesting that most ammonium produced through OM remineralization is rapidly sorbed to sediment or transformed through nitrification. Nitrate was detected in the porewater samples, but at concentrations that would have been diluted to below the detection limit during the KCl extraction process used for this study. Ammonium sorbed to sediment is not as readily depleted by uptake or removed by transport compared to dissolved nitrate. Thus, it is not surprising that inorganic N may accumulate predominantly in a less mobile or available form in this highly oligotrophic system. It is unclear how often and under what conditions ammonium desorption from the hyporheic sediments can occur. Potentially, during low flows, weathering-derived cations that accumulate in hyporheic porewater could exchange with sorbed ammonium, releasing it into the porewater (Yan et al., 2018). If this occurs regularly, the pool of sorbed ammonium could act as a large temporary store of inorganic N for downstream ecosystems (Day & Hall, 2017; Gómez et al., 2009), increasing the long-term N availability of the system (Triska et al., 1994). This hyporheic pool of inorganic N is relatively large compared to surfacewater DIN pools, and supports the hypothesis that autochthonous POM spiraling in MDV streams provides N subsidies to downstream microbial mats (Kohler et al., 2018).

In MDV streams, where daily flood pulses mobilize POM from microbial mats and the DOM concentrations are quite low, POM may account for a higher proportion of the total stream organic matter compared to other oligotrophic systems (e.g., Jones et al., 1995a). The absence of detectable extractable humic material in many of the hyporheic sediment samples is consistent with the low DOM concentrations and low humic percentage in the streams (Aiken et al., 1996). The limited sediment samples with higher extractable humic material may have been from locations in the hyporheic zone where the sediments were enriched in iron oxides on mineral surfaces that would enhance sorption of humic material.

In MDV streams, all indicators of POM processing that we measured point toward the retention of autochthonous POM in the hyporheic zone. In other systems, where allochthonous inputs are important for stream metabolism, this is not the case (Battin et al., 2008). However, we suggest that biogenic silica may be a powerful tracer of autochthonous POM that could be used in the hyporheic zones of many stream ecosystems, because diatoms are more likely to be associated with autochthonous POM than allochthonous inputs. We caution, however, that diatom community composition, available through databases such as Diatoms of North America ([diatoms.org](http://diatoms.org)), should be used to determine the source of the biogenic silica and associated POM, given the potential inputs of terrestrial soil diatoms (Antonelli et al., 2017) and silica phytoliths from plants (Carey & Fulweiler, 2012), which are not likely significant in the MDV streams. In addition, the same source modeling approach used in this study could be applied in other systems that receive both autochthonous and allochthonous inputs of organic matter to resolve the different sources of diatoms and POM entering the hyporheic zone.

### 4.3. Spatial Patterns in POM Retention and Processing

The combination of hyporheic sediment chemistry and diatom composition indicates spatial variation in autochthonous POM retention and processing across the stream channel. We propose that autochthonous POM is retained and processed the most in the hyporheic sediments beneath the intermediate lateral positions 2 and 4 (Figure 5). These intermediate regions are regularly connected to surface waters, unlike the more distal edge positions that are inundated infrequently. In addition, POM deposited at these intermediate regions may have a longer residence time than POM deposited in the thalweg, where continual flow may regularly flush POM further downstream. The intermediate sites thus are best poised to act as permanent ecosystem control points (Bernhardt et al., 2017), with both frequent pulses of reactants and the conditions necessary for biogeochemical transformations. This finding is relevant for intermittent streams in other ecosystems; certain regions of the hyporheic zone may remain saturated and poised for biogeochemical

transformations (Burrows et al., 2017), while other regions may become disconnected from surface water or be regularly flushed by daily or seasonal flood pulses.

We predicted that geomorphic units (i.e., pools, riffles, and meanders) would differ in the retention of POM, with higher retention in depositional environments of pools and the inner banks of meanders. We found some support of our prediction as pools and meanders had higher values of chlorophyll *a*, pools had higher concentrations of sorbed ammonium, and the intermediate lateral positions of pools and the inner banks of meanders had the highest percent biogenic silica and LOI (Figure 4). The finding that pools are locations of elevated POM processing is supported by previous research in temperate locations: pools tend to receive more POM from surface water and also process POM more quickly (Burrows et al., 2017; Hendricks, 1993). The lack of strong differences between geomorphic units may be due to the relatively moderate differences in stream channel morphology and lack of deep pools or cutbank erosion. Alternatively, our findings may be due to the simplicity of our sampling design with only one lateral transect per riffle, pool, and meander. Whereas downwelling may dominate at the heads of riffles, upwelling can occur in riffle-pool transitions, dynamics that would have been more apparent with a longitudinal sampling design (Hill et al., 1998). Given the high spatial heterogeneity in hyporheic sediments, denser sampling strategies may reveal more geomorphic control on rates of POM processing in MDV streams.

## 5. Conclusions

Our results demonstrate that the composition and quantity of diatom frustules can be used to identify both the source of autochthonous POM and stable locations of POM retention and processing in hyporheic sediments. Elevated biogenic silica, which indicates an accumulation of diatom frustules, was associated with higher concentrations of organic matter and sorbed ammonium, suggesting that certain locations within the hyporheic zone are relatively stable locations of autochthonous POM entrainment and remineralization. The composition of hyporheic diatom assemblages supported the hypothesis that N-fixing mats are an important source of autochthonous POM to the hyporheic zone, allowing for the remineralization of N-fixing mat material and potential downstream uptake of inorganic N. Our results suggest that autochthonous POM processing occurs most readily at sites located between the thalweg and the wetted margin where hyporheic sediments are routinely supplied with POM but do not experience continual flushing, a finding that may apply to intermittent streams in other environments. Our findings also suggest that large-scale geomorphic settings such as pools and riffles are not as important as lateral position across the stream channel in determining POM input to the hyporheic zone, but this warrants additional study. Our novel use of diatom frustules as tracers of POM source and processing in MDV hyporheic sediments highlights the importance of autochthonous POM in this system, suggesting that autochthonous POM may be critical for downstream ecosystems in other freshwater systems as well. Where possible, we propose the use of diatoms as temporally stable indicators of POM retention in freshwater hyporheic zones.

## Data Availability Statement

The hyporheic sediment data set is available at Heindel et al. (2021) (<https://doi.org/10.6073/pasta/3f76c-cdf3d330df54aed1aee815dab23>) and the diatom composition data set at Darling et al. (2021) (<https://doi.org/10.6073/pasta/21650245acdf99704b4571b887fdeb2a>). Both data sets are available at the McMurdo Long-Term Ecological Research website ([mcm.lternet.edu](http://mcm.lternet.edu)) and the Environmental Data Initiative.

## Acknowledgments

Funding for this work was provided by a U.S. National Science Foundation grant to the McMurdo Dry Valleys Long-Term Ecological Research project (Grant no. #OPP-1637708). The authors would like to thank the Antarctic Support Contract and Petroleum Helicopters, Inc. for logistics support and transportation that made this fieldwork possible.

## References

- Aiken, G., McKnight, D., Harnish, R., & Wershaw, R. (1996). Geochemistry of aquatic humic substances in the Lake Fryxell Basin, Antarctica. *Biogeochemistry*, 34(3), 157–188. <https://doi.org/10.1007/BF00000900>
- Anderson, M. J. (2001). A new method for non-parametric multivariate analysis of variance. *Austral Ecology*, 26, 32–46. <https://doi.org/10.1111/j.1442-9993.2001.01070.pp.x>
- Andriuzzi, W. S., Stanish, L. F., Simmons, B. L., Jaros, C., Adams, B. J., Wall, D. H., & McKnight, D. M. (2018). Spatial and temporal patterns of microbial mats and associated invertebrates along an Antarctic stream. *Polar Biology*, 41(10), 1911–1921. <https://doi.org/10.1007/s00300-018-2331-4>
- Antonelli, M., Wetzel, C. E., Ector, L., Teuling, A. J., & Pfister, L. (2017). On the potential for terrestrial diatom communities and diatom indices to identify anthropic disturbance in soils. *Ecological Indicators*, 75, 73–81. <https://doi.org/10.1016/j.ecolind.2016.12.003>

- Ball, B. A., & Virginia, R. A. (2014). The ecological role of moss in a polar desert: implications for aboveground–belowground and terrestrial–aquatic linkages. *Polar Biology*, 37(5), 651–664. <https://doi.org/10.1007/s00300-014-1465-2>
- Barrett, J. E., Virginia, R. A., & Wall, D. H. (2002). Trends in resin and KCl-extractable soil nitrogen across landscape gradients in Taylor Valley, Antarctica. *Ecosystems*, 5(3), 289–299. <https://doi.org/10.1007/s10021-001-0072-6>
- Bartoň, K. (2020). *MuMIn: Multi-Model inference. R package version 1.43.17*. Retrieved from <https://CRAN.R-project.org/package=MuMIn>
- Battin, T. J., Kaplan, L. A., Findlay, S., Hopkinson, C. S., Marti, E., Packman, A. I., et al. (2008). Biophysical controls on organic carbon fluxes in fluvial networks. *Nature Geoscience*, 1(2), 95–100. <https://doi.org/10.1038/ngeo101>
- Battin, T. J., Luyssaert, S., Kaplan, L. A., Aufdenkampe, A. K., Richter, A., & Tranvik, L. J. (2009). The boundless carbon cycle. *Nature Geoscience*, 2(9), 598–600. <https://doi.org/10.1038/ngeo618>
- Berger, G. W., Doran, P. T., & Thomsen, K. J. (2013). Micro-hole and multigrain quartz luminescence dating of Paleodeltas at Lake Fryxell, McMurdo Dry Valleys (Antarctica), and relevance for lake history. *Quaternary Geochronology*, 18, 119–134. <https://doi.org/10.1016/j.quageo.2013.04.002>
- Bergstrom, A., Jencso, K., & McGlynn, B. (2016). Spatiotemporal processes that contribute to hydrologic exchange between hillslopes, valley bottoms, and streams. *Water Resources Research*, 52(6), 4628–4645. <https://doi.org/10.1002/2015WR017972>
- Bernhardt, E. S., Blaszczyk, J. R., Ficken, C. D., Fork, M. L., Kaiser, K. E., & Seybold, E. C. (2017). Control points in ecosystems: Moving beyond the hot spot hot moment concept. *Ecosystems*, 20(4), 665–682. <https://doi.org/10.1007/s10021-016-0103-y>
- Blanco, S., Álvarez, I., & Cejudo, C. (2008). A test on different aspects of diatom processing techniques. *Journal of Applied Phycology*, 20(4), 445–450. <https://doi.org/10.1007/s10811-007-9292-2>
- Boano, F., Camporeale, C., Revelli, R., & Ridolfi, L. (2006). Sinuosity-driven hyporheic exchange in meandering rivers. *Geophysical Research Letters*, 33(18), L18406. <https://doi.org/10.1029/2006GL027630>
- Burkins, M. B., Virginia, R. A., & Wall, D. H. (2001). Organic carbon cycling in Taylor Valley, Antarctica: Quantifying soil reservoirs and soil respiration. *Global Change Biology*, 7(1), 113–125. <https://doi.org/10.1046/j.1365-2486.2001.00393.x>
- Burrows, R. M., Rutledge, H., Bond, N. R., Eberhard, S. M., Auhl, A., Andersen, M. S., et al. (2017). High rates of organic carbon processing in the hyporheic zone of intermittent streams. *Scientific Reports*, 7(1), 13198. <https://doi.org/10.1038/s41598-017-12957-5>
- Cardenas, M. B., Wilson, J. L., & Zlotnik, V. A. (2004). Impact of heterogeneity, bed forms, and stream curvature on subchannel hyporheic exchange. *Water Resources Research*, 40(8), W08307. <https://doi.org/10.1029/2004WR003008>
- Carey, J. C., & Fulweiler, R. W. (2012). The terrestrial silica pump. *PloS One*, 7(12), e52932. <https://doi.org/10.1371/journal.pone.0052932>
- Chan, Y. (2011). *Biogenic silica analysis. LACCORE: National Lacustrine Core Facility*. Retrieved from <http://lrc.geo.umn.edu/laccore/assets/pdf/sops/Biogenic%20Silica%20SOP%202011.pdf>
- Conovitz, P. A., Mcknight, D. M., Macdonald, L. H., Fountain, A. G., & House, H. R. (1998). Hydrologic processes influencing streamflow variation in Fryxell Basin, Antarctica. *Ecosystem dynamics in a polar desert: The McMurdo Dry Valleys* (pp. 93–108). Antarctica: American Geophysical Union (AGU). <https://doi.org/10.1029/AR072p0093>
- Cullis, J. D. S., Stanish, L. F., & 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(1), 86–97. <https://doi.org/10.1002/2013WR014061>
- Cushing, C. E., Minshall, G. W., & Newbold, J. D. (1993). Transport dynamics of fine particulate organic matter in two Idaho streams. *Limnology & Oceanography*, 38(6), 1101–1115. <https://doi.org/10.4319/lo.1993.38.6.1101>
- Dahm, C. N., Baker, M. A., Moore, D. I., & Thibault, J. R. (2003). Coupled biogeochemical and hydrological responses of streams and rivers to drought. *Freshwater Biology*, 48(7), 1219–1231. <https://doi.org/10.1046/j.1365-2427.2003.01082.x>
- Darling, J., Heindel, R. C., Singley, J. G., Bergstrom, A. J., Mcknight, D. M. (2021). *Hyporheic diatom community assemblages from Von Guerard stream, Taylor Valley, McMurdo Dry Valleys, Antarctica in January 2019*. Environmental Data Initiative. <https://doi.org/10.6073/pasta/21650245acdf99704b4571b887fdeb2a>
- Day, N. K., & Hall, R. O. (2017). Ammonium uptake kinetics and nitrification in mountain streams. *Freshwater Science*, 36(1), 41–54. <https://doi.org/10.1086/690600>
- DeMaster, D. J. (1981). The supply and accumulation of silica in the marine environment. *Geochimica et Cosmochimica Acta*, 45(10), 1715–1732. [https://doi.org/10.1016/0016-7037\(81\)90006-5](https://doi.org/10.1016/0016-7037(81)90006-5)
- Dodds, W. K., Gudder, D. A., & Mollenhauer, D. (1995). The ecology of Nostoc. *Journal of Phycology*, 31(1), 2–18. <https://doi.org/10.1111/j.0022-3646.1995.00002.x>
- Drummond, J. D., Aubeneau, A. F., & Packman, A. I. (2014). Stochastic modeling of fine particulate organic carbon dynamics in rivers. *Water Resources Research*, 50(5), 4341–4356. <https://doi.org/10.1002/2013WR014665>
- Drummond, J. D., Larsen, L. G., González-Pinzón, R., Packman, A. I., & Harvey, J. W. (2017). Fine particle retention within stream storage areas at base flow and in response to a storm event. *Water Resources Research*, 53(7), 5690–5705. <https://doi.org/10.1002/2016WR020202>
- Esposito, R. M. M., Horn, S. L., McKnight, D. M., Cox, M. J., Grant, M. C., Spaulding, S. A., et al. (2006). Antarctic climate cooling and response of diatoms in glacial meltwater streams. *Geophysical Research Letters*, 33(7), L07406. <https://doi.org/10.1029/2006GL025903>
- Esposito, R. M. M., Spaulding, S. A., McKnight, D. M., Van de Vijver, B., Kopalová, K., Lubinski, D., et al. (2008). Inland diatoms from the McMurdo Dry Valleys and James Ross Island, Antarctica. *Botany*, 86(12), 1378–1392. <https://doi.org/10.1139/B08-100>
- Fellman, J. B., Dogramaci, S., Skrzypek, G., Dodson, W., & Grierson, P. F. (2011). Hydrologic control of dissolved organic matter biogeochemistry in pools of a subtropical dryland river. *Water Resources Research*, 47(6), W06501. <https://doi.org/10.1029/2010WR010275>
- Fenoglio, S., Bo, T., Cammarata, M., López-Rodríguez, M. J., & Tierno de Figueroa, J. M. (2015). Seasonal variation of allochthonous and autochthonous energy inputs in an alpine stream. *Journal of Limnology*, 74(2), 272–277. <https://doi.org/10.4081/jlimnol.2014.1082>
- Findlay, S. (1995). Importance of surface-subsurface exchange in stream ecosystems: The hyporheic zone. *Limnology & Oceanography*, 40(1), 159–164. <https://doi.org/10.4319/lo.1995.40.1.0159>
- Fountain, A. G., Nylen, T. H., Monaghan, A., Basagic, H. J., & Bromwich, D. (2010). Snow in the McMurdo Dry Valleys, Antarctica. *International Journal of Climatology*, 30(5), 633–642. <https://doi.org/10.1002/joc.1933>
- Gabor, R. S., Burns, M. A., Lee, R. H., Elg, J. B., Kemper, C. J., Barnard, H. R., & McKnight, D. M. (2015). Influence of leaching solution and catchment location on the fluorescence of water-soluble organic matter. *Environmental Science & Technology*, 49(7), 4425–4432. <https://doi.org/10.1021/es504881t>
- Geyer, K. M., Altrichter, A. E., Horn, D. J. V., Takacs-Vesbach, C. D., Gooseff, M. N., & Barrett, J. E. (2013). Environmental controls over bacterial communities in polar desert soils. *Ecosphere*, 4(10), art127. <https://doi.org/10.1890/ES13-00048.1>
- Gómez, R., García, V., Vidal-Abarca, R., & Suárez, L. (2009). Effect of intermittency on N spatial variability in an arid Mediterranean stream. *Journal of the North American Benthological Society*, 28(3), 572–583. <https://doi.org/10.1899/09-016.1>

- Gooseff, M. N., & McKnight, D. M. (2021). High frequency seasonal stream gage measurements from Von Guerard Stream at F6 in Taylor Valley, McMurdo Dry Valleys, Antarctica from 1990 to present. *Environmental Data Initiative*. <https://doi.org/10.6073/pasta/f0ae43b1f92bf7a17e187a1d0e130dce>
- Gooseff, M. N., McKnight, D. M., Lyons, W. B., & 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), 1–17. <https://doi.org/10.1029/2001WR000834>
- Gooseff, M. N., McKnight, D. M., Runkel, R. L., & Duff, J. H. (2004). Denitrification and hydrologic transient storage in a glacial meltwater stream, McMurdo Dry Valleys, Antarctica. *Limnology & Oceanography*, 49(5), 1884–1895. <https://doi.org/10.4319/lo.2004.49.5.1884>
- Gooseff, M. N., Wlostowski, A. N., McKnight, D. M., & Jaros, C. (2017). Hydrologic connectivity and implications for ecosystem processes—Lessons from naked watersheds. *Geomorphology*, 277, 63–71. <https://doi.org/10.1016/j.geomorph.2016.04.024>
- Hall, R. O., Tank, J. L., Baker, M. A., Rosi-Marshall, E. J., & Hotchkiss, E. R. (2016). Metabolism, gas exchange, and carbon spiraling in rivers. *Ecosystems*, 19(1), 73–86. <https://doi.org/10.1007/s10021-015-9918-1>
- Harvey, J., & Gooseff, M. (2015). River corridor science: Hydrologic exchange and ecological consequences from bedforms to basins. *Water Resources Research*, 51(9), 6893–6922. <https://doi.org/10.1002/2015WR017617>
- Hatton, J. E., Hendry, K. R., Hirst, C., Opfergelt, S., Henkel, S., Silva-Busso, A., et al. (2020). Silicon isotopic composition of dry and wet-based glaciers in Antarctica. *Frontiers in Earth Sciences*, 8, 286. <https://doi.org/10.3389/feart.2020.00286>
- Heindel, R. C., Singley, J. G., Bergstrom, A. J., Darling, J., Welch, K. A., McKnight, D. M., & Gooseff, M. N. 2021. Hyporheic sediment characteristics from Von Guerard stream, Taylor Valley, McMurdo Dry Valleys, Antarctica in January 2019. Environmental Data Initiative. <https://doi.org/10.6073/pasta/3f76ccdf3d330df54aed1aee815dab23>
- Hendricks, S. P. (1993). Microbial ecology of the hyporheic zone: A perspective integrating hydrology and biology. *Journal of the North American Benthological Society*, 12(1), 70–78. <https://doi.org/10.2307/1467687>
- Hill, A. R., Labadia, C. F., & Sanmugadas, K. (1998). Hyporheic zone hydrology and nitrogen dynamics in relation to the streambed topography of a N-rich stream. *Biogeochemistry*, 42(3), 285–310. <https://doi.org/10.1023/A:1005932528748>
- Hirst, C., Opfergelt, S., Gaspard, F., Hendry, K. R., Hatton, J. E., Welch, S., et al. (2020). Silicon isotopes reveal a non-glacial source of silicon to crescent stream, McMurdo Dry Valleys, Antarctica. *Frontiers in Earth Science*, 8, 229. <https://doi.org/10.3389/feart.2020.00229>
- Hodgson, D. A., Vyverman, W., Verleyen, E., Sabbe, K., Leavitt, P. R., Taton, A., et al. (2004). Environmental factors influencing the pigment composition of in situ benthic microbial communities in east Antarctic lakes. *Aquatic Microbial Ecology*, 37(3), 247–263. <https://doi.org/10.3354/ame037247>
- Holm-Hansen, O., Lorenzen, C. J., Holmes, R. W., & Strickland, J. D. H. (1965). Fluorometric determination of chlorophyll. *ICES Journal of Marine Science*, 30(1), 3–15. <https://doi.org/10.1093/icesjms/30.1.3>
- Howard-Williams, C., Priscu, J. C., & Vincent, W. F. (1989). Nitrogen dynamics in two antarctic streams. *Hydrobiologia*, 172(1), 51–61. <https://doi.org/10.1007/BF00031612>
- Hurvich, C. M., & Tsai, C.-L. (1989). Regression and time series model selection in small samples. *Biometrika*, 76(2), 297–307. <https://doi.org/10.1093/biomet/76.2.297>
- Jones, J. B., Fisher, S. G., & Grimm, N. B. (1995a). Vertical hydrologic exchange and ecosystem metabolism in a Sonoran Desert Stream. *Ecology*, 76(3), 942–952. <https://doi.org/10.2307/1939358>
- Jones, J. B., Fisher, S. G., & Grimm, N. B. (1995b). Nitrification in the hyporheic zone of a desert stream ecosystem. *Journal of the North American Benthological Society*, 14(2), 249–258. <https://doi.org/10.2307/1467777>
- Kloep, F., & Röske, I. (2004). Transport of algal cells in hyporheic sediments of the River Elbe (Germany). *International Review of Hydrobiology*, 89(1), 88–101. <https://doi.org/10.1002/iroh.200310662>
- Knights, D., Kuczynski, J., Charlson, E. S., Zaneveld, J., Mozer, M. C., Collman, R. G., et al. (2011). Bayesian community-wide culture-independent microbial source tracking. *Nature Methods*, 8(9), 761–763. <https://doi.org/10.1038/nmeth.1650>
- Kohler, T. J., Stanish, L. F., Liptzin, D., Barrett, J. E., & McKnight, D. M. (2018). Catch and release: Hyporheic retention and mineralization of N-fixing *Nostoc* sustains downstream microbial mat biomass in two polar desert streams: Autochthonous nitrogen cycling in two Antarctic streams. *Limnology and Oceanography Letters*, 3(4), 357–364. <https://doi.org/10.1002/lo.21008>
- Levy, J. (2012). How big are the McMurdo Dry Valleys? Estimating ice-free area using Landsat image data. *Antarctic Science*, 25(1), 119–120. <https://doi.org/10.1017/S0954102012000727>
- Lisle, T. E., & Hilton, S. (1999). Fine bed material in pools of natural gravel bed channels. *Water Resources Research*, 35(4), 1291–1304. <https://doi.org/10.1029/1998WR900088>
- Louda, J. W., Li, J., Liu, L., Winfree, M. N., & Baker, E. W. (1998). Chlorophyll-a degradation during cellular senescence and death. *Organic Geochemistry*, 29(5), 1233–1251. [https://doi.org/10.1016/S0146-6380\(98\)00186-7](https://doi.org/10.1016/S0146-6380(98)00186-7)
- Maurice, P. A., McKnight, D. M., Leff, L., Fulghum, J. E., & Gooseff, M. (2002). Direct observations of aluminosilicate weathering in the hyporheic zone of an Antarctic Dry Valley stream. *Geochimica et Cosmochimica Acta*, 66(8), 1335–1347. [https://doi.org/10.1016/S0016-7037\(01\)00890-0](https://doi.org/10.1016/S0016-7037(01)00890-0)
- Mazerolle, M. J. (2020). *AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c)*. R package version 2.3-1. Retrieved from <https://cran.r-project.org/package=AICcmodavg>
- McKnight, D. M., Runkel, R. L., Tate, C. M., Duff, J. H., & 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(2), 171–188. [https://doi.org/10.1899/0887-3593\(2004\)023<0171:INAPDO>2.0.CO;2](https://doi.org/10.1899/0887-3593(2004)023<0171:INAPDO>2.0.CO;2)
- Newbold, J. D., Thomas, S. A., Minshall, G. W., Cushing, C. E., & Georgian, T. (2005). Deposition, benthic residence, and resuspension of fine organic particles in a mountain stream. *Limnology & Oceanography*, 50(5), 1571–1580. <https://doi.org/10.4319/lo.2005.50.5.1571>
- Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., et al. (2019). *vegan: Community Ecology Package*. R package version 2.5-6. Retrieved from <https://CRAN.R-project.org/package=vegan>
- Power, S. N., Salvatore, M. R., Sokol, E. R., Stanish, L. F., & Barrett, J. E. (2020). Estimating microbial mat biomass in the McMurdo Dry Valleys, Antarctica using satellite imagery and ground surveys. *Polar Biology*, 43(11), 1753–1767. <https://doi.org/10.1007/s00300-020-02742-y>
- Shumilova, O., Zak, D., Datry, T., von Schiller, D., Corti, R., Foulquier, A., et al. (2019). Simulating rewetting events in intermittent rivers and ephemeral streams: A global analysis of leached nutrients and organic matter. *Global Change Biology*, 25(5), 1591–1611. <https://doi.org/10.1111/gcb.14537>
- Simmons, B. L., Wall, D. H., Adams, B. J., Ayres, E., Barrett, J. E., & Virginia, R. A. (2009). Long-term experimental warming reduces soil nematode populations in the McMurdo Dry Valleys, Antarctica. *Soil Biology & Biochemistry*, 41(10), 2052–2060. <https://doi.org/10.1016/j.soilbio.2009.07.009>



- Spaulding, S., Esposito, R., Lubinski, D., Horn, S., Cox, M., McKnight, D. et al. (2020). Antarctic Freshwater Diatoms web site, McMurdo Dry Valleys LTER. visited 11 Sep 2020 Retrieved from <https://huey.colorado.edu/diatoms/>
- Spaulding, S. A., McKnight, D. M., Stoermer, E. F., & 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.
- Stanish, L. F. (2011). *Ecological controls on stream diatom communities in the McMurdo Dry Valleys, Antarctica*. Boulder, CO: University of Colorado at Boulder.
- Stanish, L. F., Kohler, T. J., Esposito, R. M. M., Simmons, B. L., Nielsen, U. N., Wall, D. H., et al. (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. <https://doi.org/10.1139/F2012-022>
- Tank, J. L., Rosi-Marshall, E. J., Griffiths, N. A., Entekin, S. A., & Stephen, M. L. (2010). A review of allochthonous organic matter dynamics and metabolism in streams. *Journal of the North American Benthological Society*, 29(1), 118–146. <https://doi.org/10.1899/08-170.1>
- Tonina, D., & Buffington, J. M. (2009). Hyporheic exchange in mountain rivers I: Mechanics and environmental effects. *Geography Compass*, 3(3), 1063–1086. <https://doi.org/10.1111/j.1749-8198.2009.00226.x>
- Triska, F. J., Jackman, A. P., Duff, J. H., & Avanzino, R. J. (1994). Ammonium sorption to channel and riparian sediments: A transient storage pool for dissolved inorganic nitrogen. *Biogeochemistry*, 26(2), 67–83. <https://doi.org/10.1007/BF02182880>
- Valet, H. M., Fisher, S. G., Grimm, N. B., & Camill, P. (1994). Vertical hydrologic exchange and ecological stability of a desert stream ecosystem. *Ecology*, 75(2), 548–560. <https://doi.org/10.2307/1939557>
- Wetzel, R. G., & Likens, G. E. (2013). *Limnological analyses*. Springer Science & Business Media.
- Witherow, R. A., Lyons, W. B., Bertler, N. A. N., Welch, K. A., Mayewski, P. A., Sneed, S. B., et al. (2006). The aeolian flux of calcium, chloride and nitrate to the McMurdo Dry Valleys landscape: Evidence from snow pit analysis. *Antarctic Science*, 18(4), 497–505. <https://doi.org/10.1017/S095410200600054X>
- Wlostowski, A. N., Gooseff, M. N., McKnight, D. M., Jaros, C., & Lyons, W. B. (2016). Patterns of hydrologic connectivity in the McMurdo Dry Valleys, Antarctica: A synthesis of 20 years of hydrologic data: Connectivity of Glacier-Stream-Lake Systems in the McMurdo Dry Valleys. *Hydrological Processes*, 30(17), 2958–2975. <https://doi.org/10.1002/hyp.10818>
- Wlostowski, A. N., Gooseff, M. N., McKnight, D. M., & Lyons, W. B. (2018). Transit times and rapid chemical equilibrium explain chemostasis in glacial meltwater streams in the McMurdo Dry Valleys, Antarctica. *Geophysical Research Letters*, 45(24), 13322–13331. <https://doi.org/10.1029/2018GL080369>
- Yan, A., Liu, C., Liu, Y., & Xu, F. (2018). Effect of ion exchange on the rate of aerobic microbial oxidation of ammonium in hyporheic zone sediments. *Environmental Science and Pollution Research*, 25(9), 8880–8887. <https://doi.org/10.1007/s11356-018-1217-x>
- Zeglin, L. H., Dahm, C. N., Barrett, J. E., Gooseff, M. N., Fitzpatrick, S. K., & Takacs-Vesbach, C. D. (2011). Bacterial community structure along moisture gradients in the Parafluvial sediments of two ephemeral desert streams. *Microbial Ecology*, 61(3), 543–556. <https://doi.org/10.1007/s00248-010-9782-7>