Catch and release: Hyporheic retention and mineralization of N-fixing Nostoc sustains downstream microbial mat biomass in two polar desert streams

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Abstract

Much work has been performed to investigate controls on nitrogen (N) uptake in streams, yet the fate of assimilated N is comparatively poorly resolved. Here, we use in-stream fixed N as an isotopic tracer to study the fate of assimilated N in glacial meltwater streams. We characterized δ15N signatures of Oscillatorean, Chlorophyte, and N-fixing Nostoc mats over the lengths of two streams, and transported particulate organic matter (POM) in one. POM was isotopically most similar to Nostoc, which always had values near the atmospheric standard (δ15N ≈ 0‰), suggesting N-fixation. Other mat types were depleted upstream, and became progressively enriched downstream (plateauing at δ15N ≈ 0‰), indicating a shift in N source. These results collectively show that Nostoc-derived N is mobilized, mineralized, and increasingly assimilated downstream as more depleted glacier-derived N is exhausted, demonstrating the importance of organic matter processing to balancing elemental budgets, and improving our understanding of nutrient cycling in lotic environments.

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Data Availability Statement: Data are available through the Environmental Data Initiative repository (https://portal.edirepository.org/nis/map-browse?packageid=knblter-mcm.9031.2).

Additional Supporting Information may be found in the online version of this article.

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Nutrient spiraling provides a framework for conceptualizing how nutrients cycle through streams (Newbold et al. 1981). Each “nutrient spiral” begins with the transport of a dissolved inorganic nutrient through the water column, continues with its uptake and storage in the streamed and/or underlying hyporheic zone, and ends with its release back into the water column in inorganic form. The average distance required for the completion of one spiral (i.e., the “spiral length”) provides a means for comparing nutrient dynamics across streams. In the case of nitrogen (N), tracer studies from the Lotic Intersite Nitrogen eXperiments (LINX) demonstrated the shortest spiral lengths occur at headwaters (indicating high processing rates), with less than half of all N inputs exported downstream (Peterson et al. 2001). While this is partially due to removal by denitrification, most N is assimilated by biota and stored as organic matter (OM) in the streamed or the hyporheic zone (Mulholland et al. 2008). Exchange with the hyporheic zone brings N that has been assimilated, stored, and degraded back into the water column, making it available for re-uptake (Jones et al. 1995a,b), and can thus be critical component of N cycling across landscapes.

Microbial phototrophs are often responsible for the majority of N uptake (Hall et al. 2009; Tank et al. 2018), and given the likely greater lability of microbial OM compared to allochthonous OM, they may disproportionally contribute to nutrient release following mineralization in the hyporheic zone (e.g., Jones et al. 1995b). Yet, separating autochthonous from allochthonous contributions is challenging, and studies explicitly investigating the downstream fate of N following autotrophic uptake are scarce (e.g., O’Brien et al. 2012; Johnson et al. 2013). In addition to uptake, some stream auto- trophs (e.g., heterocystous cyanobacteria) contribute “new” N by fixing N₂ from the atmosphere, which can be an important flux in N-limited systems (Grimm and Petrone 1997; Kunza and Hall 2014). Given the characteristic isotopic signature of freshly-fixed N ($\delta^{15}N \approx 0\%_{\text{oo}}$, Michener and Lajtha 2007), it may be possible to use this isotope ratio as a tracer to investigate the downstream fate of assimilated N, which may not be captured by short-term experiments at reach scales.

The streams of the McMurdo Dry Valleys are excellent end-member systems for studying the dynamics of autochthonous OM because stream water is derived from glacial melt (McKnight et al. 1999), and particulate organic matter (POM) generation is an exclusively autochthonous process derived from microbial mats due to the plant-free landscape (Cullis et al. 2014). Thus, all N entering the water column and hyporheic zone is derived from glacier runoff or in-stream N-fixation (Howard-Williams et al. 1989). Furthermore, coupled hydrologic and biogeochemical processes have been well-characterized in Dry Valley streams. The greater shear stresses acting on the streamed during the daily flow pulse produce greater concentrations of POM on the rising limb of the hydrograph (Cullis et al. 2014). The strong influence of hyporheic zone processes is evidenced by downstream increases in dissolved silica due to mineral weathering and rapid hyporheic exchange (Gooseff et al. 2002). Further, reactive transport modeling and nitrate tracer experiments similar to the LINX studies have demonstrated the hyporheic zone to be a hotspot of N cycling (Gooseff et al. 2004).

Some McMurdo Dry Valleys streams can sustain high mat biomass far from the glacier source, although water column nitrate concentrations are typically low or undetectable in streams with abundant mats (McKnight et al. 2007). However, nitrate concentrations can be much greater in the hyporheic zone (McKnight et al. 2004), and given the observed coupling of OM and N transformations, it may be that hyporheic zone nitrate accumulates from respiration/nitrification of mat-produced dissolved organic matter (McKnight et al. 2004) or retained mat material (Koch et al. 2010) as in the classic studies of desert streams (Jones et al. 1995a). Overall, given the limited input of glacier-derived N, high mat biomass and uptake, daily movement of mat-derived POM, and extensive hyporheic zone interactions, we hypothesize that the mineralization of fixed N facilitates productivity in these N-limited streams, and that the cumulative effects of these processes will be reflected in the isotopic signatures of mats downstream.

To test our hypothesis, we capitalized on the different $\delta^{15}N$ signatures of potential N sources to demonstrate the dynamic downstream impact of mineralized autochthonous N. Nitrate accumulates on McMurdo Dry Valleys glaciers from atmospheric deposition, and is characteristically depleted in $\delta^{15}N$ (from $-9.5\%_{\text{oo}}$ to $-26.2\%_{\text{oo}}$, Michalski et al. 2005), providing a natural abundance tracer for glacier-derived N. Of the available OM sources, N-fixing mat communities should have isotopic signatures near the atmospheric standard ($\delta^{15}N \approx 0\%_{\text{oo}}$), while non-fixing communities should reflect the signature of N available for uptake (Michener and Lajtha 2007). Accordingly, our study had two parts: First, we sampled POM transported in the water column over a diel flow cycle in one stream (Cullis et al. 2014) to evaluate its source and detect possible immobilization of N (e.g., Webster and Benfield 1986). Second, three types of microbial mats (Nostoc, Chlorophytes, and Oscillatorean) were sampled from established transects of this stream and its neighboring tributary to assess longitudinal patterns in $\delta^{15}N$. By using fixed N as a natural tracer, this work demonstrates the importance of assimilated N to balancing stream nutrient budgets, and shows that these inputs dominate the dissolved N pool after several hundred meters in these simple stream ecosystems.

**Materials and methods**

**Site description**

McMurdo Dry Valleys stream ecosystems have been studied for decades (e.g., Howard-Williams et al. 1989; McKnight et al. 1999).
et al. 1998, 2004; Kohler et al. 2015), and a subset are monitored by the McMurdo Long-Term Ecological Research (MCMLTER) program (www.mcmlter.org). Resident microbial mats are perennial (McKnight et al. 1999), and can be visually identified according to their dominant taxa. Three “mat types” are distinguished (Kohler et al. 2015): “Black” mats of N-fixing Nostoc grow on unconsolidated sediments at stream margins where they are wetted by daily flood pulses and the underlying hyporheic zone. “Orange” and “green” mats tightly adhere to the benthic substrata within the stream channel, and are dominated by non N-fixing filamentous cyanobacteria and Chlorophytes, respectively.

Our study was conducted in Von Guerard Stream and the Relict Channel (hereafter VG and RC), which drain the Von Guerard Glacier in the Kukri Hills, and are monitored by the MCMLTER (McKnight et al. 1998, 2007; Fig. 1). Upstream reaches of VG are steep and have coarse boulder substrata, which collectively discourage mat growth. Downstream, the channel splits at an experimental diversion, with VG to the east and RC to the west. Below this point the gradient is reduced, and both VG and RC support high mat biomass in intermediate reaches, though green mats are rare in RC. VG narrows downstream and drains into Lake Fryxell near the “gage” transect, while RC merges with Harnish Creek before reaching its outlet. Both streams are likely N-limited given their low nitrate concentrations (McKnight et al. 2004, 2007) and the continuous supply of phosphorus (P) from apatite weathering (Heindel et al. 2018).

Sample collection

To examine how particulate material transported in the water column compares with different mat types, we isotopically and elementally characterized POM samples from a previously described experiment (“drift 1”; Cullis et al. 2014). Briefly, a “drift transect” was established in VG between two MCMLTER algal monitoring transects (i.e., VG middle and gage; Fig. 1). A plankton net was anchored to the streambed, and POM samples from six time points were collected onto GF/F filters over 22–23 January 2008 (see Supporting Information for more details). Adjacent mats for comparison were sampled at the drift transect on 19 December 2007 (black n = 3, orange n = 3), and were collected and processed as described for other transect mats below.

To test how downstream distance influences mat characteristics, at least three replicates of black, green, and orange mats were taken from the three established VG transects (Fig. 1; Kohler et al. 2015). Samples were collected from VG gage on 14 January 2013, and from middle and upper transects on 15 January 2013. To better resolve longitudinal patterns, duplicate (and occasionally triplicate) samples of black and orange mats were taken along seven of the established RC transects (McKnight et al. 2007) and the Harnish Stream gage on 20 January 2013 (Fig. 1). Samples were dewatered onto GF/F filters and frozen until analysis. Biomass [as ash-free dry mass (AFDM) and chlorophyll a (Chl a)] was determined as in Kohler et al. (2015), and transect distances from the Von Guerard Glacier were approximated with Google Earth.

Elemental analyses

Elemental composition (carbon [C], N, and P) and isotopic signatures (δ13C and δ15N) were measured to assess differences in nutrient storage, acquisition, and limitation among mat types. The C : N : P and isotope subsamples were dried and ground to a powder, and carbonates were removed from the C : N aliquot by fumigation. Percent C and N content was measured from this material using a CE 1500 Elemental Analyzer, and isotopic ratios were obtained with a Finnigan-MAT Delta Plus XL mass spectrometer. The %P aliquot was combusted, digested, and analyzed as orthophosphate with a Lachat QuikChem 8500 Flow Injection Analyzer.
We evaluated the possible source(s) of POM in transport by comparing its isotopic and elemental characteristics with mats collected from VG (from both 2008 and 2013) using Tukey’s Honest Significant Differences (TukeyHSD). To evaluate longitudinal patterns, we compared mat biomass, elemental composition, and isotopic signatures from VG and RC with their distance from Von Guerard Glacier. Analysis of covariance (ANCOVA) models were created by including stream (RC or VG), mat type (black, green, or orange), distance from the glacier, and the interaction between the latter two, all as fixed effects with the ln function in R. Models were simplified with the step function to remove nonsignificant terms before reporting p values (following Crawley 2013). TukeyHSD was then applied to compare mat types with each other across streams. Trend lines were fitted to data in figures using least-squares linear regression and cubic smoothing splines for VG and RC, respectively. Significance was set at α = 0.05, and all analyses were performed using R version 3.2.3 (R Core Team 2015). All data are available online through the Environmental Data Initiative repository (Kohler 2018).

**Results**

**Differences between mat types and POM**

We found mat types to differ both elementally and isotopically, suggesting that they can represent distinct sources of POM. Molar C : N differed by mat type (ANCOVA, F = 10.1, p < 0.001), and both black (TukeyHSD; p < 0.001) and green mats (p = 0.005) had greater C : N ratios than orange mats, but were not different from each other. Molar C : P (F = 15.0, p < 0.001) and N : P (F = 18.1, p < 0.001) ratios differed by mat type, and values for both ratios were greater in black than for orange (TukeyHSD; both p < 0.001), but not green, mats. Mats also differed in their δ¹³C (ANCOVA; F = 15.3, p < 0.001) and δ¹⁵N composition (F = 73.7, p < 0.001). Black mats were enriched in δ¹³C compared to orange (TukeyHSD; p = 0.007) and green (p < 0.001) mats, and orange mats enriched compared to green (p = 0.008). For δ¹⁵N, black mats had values near 0‰ as expected, and were enriched compared to orange and green mats (TukeyHSD; both p < 0.001), but orange mats were not different from green.

We found that POM in transport was isotopically most similar to black mats, and contained proportionately more N compared with other mat types, indicating the immobilization and export of predominately Nostoc-derived N downstream. POM was enriched in δ¹⁵N (ranging −1.12‰ to 0.62‰) compared to orange and green mats (Fig. 2b; both p < 0.001), but was not different from black mats. However, POM C : N ratios were lower than black (TukeyHSD; p = 0.004) and green mats (p = 0.004), though not different from orange mats (Fig. 2a). These low C : N values for POM, in combination with isotopic results, may suggest greater leaching of dissolved organic carbon compared to dissolved organic nitrogen, and/or microbial conditioning of POM resulting in immobilization of N from the water column. No significant differences were resolved between POM and the C : P or δ¹³C of any mat types.

**Longitudinal variability over VG and RC**

Black mats dominated the biomass of most transects, indicating their potential to influence N cycling (Figs. 3, 4; Supporting Information Figs. S1, S2). Both AFDM (ANCOVA; F = 27.4, p < 0.001) and Chl a (F = 27.8, p < 0.001) differed widely between mat types, with black mats having more
than double the measured biomass of orange and green mats in both streams (TukeyHSD; \( p < 0.001 \) for all). In RC, black and orange mats showed parabolic trends in abundance, being lowest upstream at the diversion, increasing to a maximum midstream, and decreasing toward Harnish gage (Fig. 4 and Supporting Information Fig. S2). Patterns were less clear for VG due to the simpler sampling regime (Fig. 3 and Supporting Information Fig. S1). The drift transect exhibited lower biomass than other transects, likely because it was sampled earlier in the flow season (i.e., December 2007; Fig. 3 and Supporting Information Fig. S1).

Longitudinal molar ratios of C : N : P indicated differences in nutrient storage, acquisition, and limitation among mat types. All mats exhibited C : N ratios above Redfield ratio (i.e., >7), indicating N scarcity, and displayed different patterns downstream (ANCOVA, \( F = 6.26, p = 0.003 \)). Black mats had C : N values between ~11 and ~12 upstream, which decreased to ~10 downstream (Figs. 3, 4). Meanwhile, orange and green mats were lower in C : N than black mats upstream (at ~8–9), and slightly increased (VG), or stayed roughly constant (RC), downstream (Figs. 3, 4). Molar C : P ratios for black mats averaged ~184, well above Redfield Ratio (i.e., 106), suggesting P limitation (Supporting Information Figs. S1, S2). Green mats exhibited balanced growth, averaging ~103, and orange mats showed P abundance, averaging ~52. Black mats also had the greatest average N : P values (~17), approximately at Redfield Ratio (i.e., 16). Conversely, green and orange mats showed evidence of N limitation, having N : P ratios averaging ~10 and ~6, respectively. C : P and N : P ratios did not exhibit longitudinal trends in either stream for any mat type (Supporting Information Figs. S1, S2).

Last, divergent, yet consistent, longitudinal patterns were present in the \( \delta^{15}N \) signatures of mats from both streams (ANCOVA, \( F = 22.2, p < 0.001 \)), reflecting downstream changes in N source and acquisition among mat types (\( F = 8.78, p < 0.001 \)). Black mats exhibited \( \delta^{15}N \) signatures near ~0‰ at all sites indicating N-fixation, while orange and green mats were more depleted in \( \delta^{15}N \) upstream (near ~5‰ or ~6‰) and became more enriched with distance from the glacier, approaching or reaching (but not surpassing) the enrichment values in black mats downstream (Figs. 3, 4). This enrichment was especially rapid in RC, and the plateau was reached within several hundred meters...
downstream from the diversion. These longitudinal patterns reflect the uptake and subsequent exhaustion of the more depleted glacially-derived N upstream, with $\delta^{15}$N signatures converging to $\sim 0\%$ as mineralized black mat material becomes increasingly available for uptake downstream.

**Discussion**

We found evidence for extensive longitudinal cycling of autochthonous OM within two McMurdo Dry Valleys streams. First, black mats maintained $\delta^{15}$N signatures near the atmospheric standard over all transects, supporting previously measured rates of N-fixation by *Nostoc* (up to 436 $\mu$mol m$^{-2}$ d$^{-1}$ in RC; McKnight et al. 2007). Second, isotopic characterization of POM reveals that N in transport is from a predominately black mat source. Furthermore, since POM C : N ratios were considerably lower than the average for black mats, their enriched $\delta^{15}$N signatures also reflect immobilization of *Nostoc*-derived N from the water column through uptake by colonizing heterotrophic microbes, analogous to leaf “conditioning” in streams (e.g., Webster and Benfield 1986). Third, orange and green mats show a progressive enrichment in $\delta^{15}$N until plateauing at $\sim 0\%$ downstream, matching the signature of black mats. Yet, mat types did not become more enriched than $\sim 0\%$, which might happen if denitrification was solely responsible for the enrichment trend (Michener and Lajtha 2007). These observations collectively suggest that N originating from N-fixation by *Nostoc* becomes available for uptake in lower reaches through the retention and mineralization of POM in the hyporheic zone, and eventually becomes the dominant source over glacially derived N following its upstream removal from the water column (Fig. 5).

Autochthonous N-fixation can contribute substantially to the N budgets of some N-limited streams (Grimm and Petrovne 1997; Kunza and Hall 2014). Yet, as reviewed by

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**Fig. 4.** Relict Channel microbial mat characteristics plotted against their distance from the Von Guerard Glacier, and includes samples collected from the experimental diversion to the Harnish Creek gage. Orange (squares) and black (circles) mats are presented as columns, and AFDM (a, b), C : N (c, d), and $\delta^{15}$N (e, f) as rows. Best-fit lines were calculated using smoothing splines. Biomass sampling was omitted for some transects lacking abundant material, which was prioritized for elemental analyses.

**Fig. 5.** Conceptual diagram illustrating reach-scale processes (a). N-fixing black mats grow at margins and generate POM during daily flood pulses, which are exported downstream. POM is mineralized in the hyporheic zone, releasing nitrate for uptake by mats and conditioned POM. Rates of these processes vary longitudinally (b), with upstream locations having the greatest concentrations of glacier-derived N and low mat biomass. As mat abundance increases downstream, glacier-derived N is exhausted, and N mineralized from black mats becomes the dominant N source. Font size indicates the hypothesized magnitude of processes at each location. Left panel adapted from Gooseff et al. (2002) and right panel from mcmlter.org.
Marcarelli et al. (2008), the subject has received only limited investigation, despite the potential of fixed N to be used as a tool for studying how N cycles through stream systems. By using stable isotopes to trace *Nostoc*-fixed N through different microbial mat types over two streams, we expand on previous studies that have demonstrated the transformation of autotroph-assimilated N to dissolved inorganic (O’Brien et al. 2012) and organic (Johnson et al. 2013) forms by revealing the dynamic impact of transport, mineralization, uptake and storage of previously assimilated N on downstream autotrophic communities.

Our results demonstrate the potential importance of N-fixation and OM cycling to sustaining autotrophic biomass in N-limited systems, and in the case of McMurdo Dry Valleys streams, help to explain how high mat abundance can be supported far from the glacier source given only limited inputs of glacier-derived N. The extent to which these patterns present themselves is inextricably linked to stream length, sediment permeability, and biomass of mat types present, with potential implications for landscape scales. While the Antarctic setting is distinct in some ways, similar conditions are observed in mid-latitude oligotrophic waters, such as in alpine (Kunza and Hall 2014) and desert (Grimm and Petrone 1997) stream systems, with the continuous flux of POM analogous to the classic studies of Sycamore Creek (e.g., Jones et al. 1995,a,b). To this end, our results underscore the importance of assimilated N to balancing stream nutrient budgets, while also highlighting longitudinal connectivity within and among microbial communities in lotic ecosystems.

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