Extreme streams: flow intermittency as a control on diatom communities in meltwater streams in the McMurdo Dry Valleys, Antarctica

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Abstract: In the McMurdo Dry Valleys of Antarctica, stream biota is limited by the brief availability of liquid water. The benthic microbial mats harbor diatoms that have adapted to hydrologic stresses, including numerous endemic species. We found a strong relationship between diatom community composition and flow intermittency in a data set including seven streams that spanned a gradient in flow intermittency. In particular, two genera represented by numerous endemic species in Dry Valley habitats, *Hantzschia* and *Luticola*, had high abundances in moderately and highly intermittent streams, respectively. The Shannon Index of diversity was greatest in streams with intermediate flow intermittency, with lower diversity in more stable streams resulting from lower evenness, and lower diversity in highly intermittent streams resulting from lower richness. These results indicate that multiple metrics of biodiversity may be useful in assessing the response of diatom communities to changing hydrologic regime. We propose that flow intermittency acts as a species filter that increases habitat heterogeneity in Dry Valley streams and may allow endemic species to persist. Future Antarctic warming may alter diatom community composition and habitats that act as refugia for desiccation-tolerant taxa.

Résumé : Dans les vallées sèches de McMurdo de l’Antarctique, les organismes des cours d’eau sont limités par la courte disponibilité d’eau liquide. Les tapis microbiens benthiques contiennent des diatomées, dont de nombreuses espèces endémiques, qui se sont adaptées aux stress hydrologiques. Il existe une forte relation entre la composition de la communauté de diatomées et l’intermittence du débit dans un ensemble de données qui inclut sept cours d’eau qui couvrent un gradient de discontinuité du débit. En particulier, deux genres qui contiennent de nombreuses espèces endémiques dans les habitats des vallées sèches, *Hantzschia* et *Luticola*, atteignent de fortes abondances, respectivement dans les cours d’eau moyennement et fortement intermittents. L’indice de diversité de Shannon est maximal dans les cours d’eau qui ont un débit modérément discontinu; la diversité est plus basse dans les cours d’eau plus stables à cause d’une équitabilité plus faible et aussi plus basse dans les cours d’eau fortement intermittents à cause d’une richesse réduite. Ces résultats indiquent que l’utilisation de plusieurs métriques de la biodiversité peuvent être utiles pour évaluer la réaction des communautés de diatomées aux changements de régime hydrologique. Nous croyons que la discontinuité du débit sert de filtre des espèces, augmente l’hétérogénéité des habitats dans les cours d’eau des vallées sèches et peut permettre aux espèces endémiques de survivre. Un réchauffement futur de l’Antarctique modifiera peut-être les communautés de diatomées et les habitats qui servent de refuges pour les taxons tolérants à la dessiccation.

[Traduit par la Rédaction]
Introduction

Desert streams are characterized by intermittent flows, which influence the structure and function of stream communities (Robson et al. 2008; Larned et al. 2010; Roelke et al. 2012). In the desert ecosystems of the McMurdo Dry Valleys of Antarctica, streambed microbial mats survive the winter months in a freeze-dried state and rapidly resume metabolism at first flows, even after years of dormancy (Vincent and Howard-Williams 1986; McKnight et al. 2007). Furthermore, stream microbial mats are important regulators of nutrient concentrations, with substantially higher nutrient concentrations found in streams with abundant mats compared with streams without visible mats (McKnight et al. 2004). Once summer glacial melt begins, stream flow changes daily and seasonally depending on the aspect, angle, and length of time solar radiation reaches the glaciers (Conovitz et al. 1998). Cold and low light conditions can reduce stream flow to a trickle and create dry patches along the stream bed that episodically desiccate the mats. The effects of flow regime are amplified owing to the lack of top-down controls, as the populations of grazing invertebrates are sparse (Virginia and Wall 1999). Thus, the Dry Valley streams provide an ideal setting to study the effect of intermittent flows on microbial biodiversity.

Similar to hot desert ecosystems (Palmer and Friedmann 1990; Moss 2010), Dry Valley stream microbial mats are dominated by filamentous cyanobacteria, with varying abundances of diatoms, chlorophytes, and other microorganisms (Alger et al. 1997). Dry Valley stream sediment bacteria also responded similarly to a hot desert stream in their sensitivity to moisture and conductivity gradients (Zeglin et al. 2011). The diatom flora has been well characterized and includes numerous endemic species from aerophilic genera commonly found in soils (Sabbe et al. 2003; Esposito et al. 2006, 2008), as well as genera that are capable of surviving dry periods (Hostetter and Hoshaw 1970). Specifically, Esposito et al. (2006) showed that endemic diatoms were more abundant in streams under low flow conditions. Thus, understanding the response of Dry Valley diatom populations to intermittent flow is relevant to understanding the response of microbial mats in desert environments, which is particularly important because changing climate and increased human demands for fresh water will intensify changes in flow regime (Poff et al. 2007; Spatharis et al. 2012).

Polar regions have experienced measurable and sometimes dramatic changes related to climate warming, such as extensive permafrost melting in the Arctic (Walvoord and Striegl 2007; Bowden et al. 2008) and recent collapses of Antarctic ice sheets (Marcott et al. 2011). However, in the McMurdo Dry Valleys, a summer cooling trend occurred from 1966 to 2000 (Doran et al. 2002). This cooling trend increased flow substantially on microbial communities in desert environments (Davey 1989; Poff 1997). In a recent study examining changes in diatom communities in the Taylor Valley over two decades, total and interannual variation in stream flow substantially influenced spatial and temporal variation in diatom community composition (Stanish et al. 2011). However, the study was conducted on productive streams that showed relatively little variation in flow intermittency. Therefore, the goal of this study is to better understand the role of flow intermittency as an environmental filter in Dry Valley streams. We evaluated changes in diatom diversity and community composition across a gradient of flow intermittency, and we hypothesized that more intermittent streams would favor desiccation-adapted taxa.

Materials and methods

Study site

The McMurdo Dry Valleys are among the coldest and driest habitats on the planet and are representative of the ice-free areas along the Antarctic coast. The Dry Valleys are located between mountain ranges that extend from the Ross Sea to the Polar Plateau (Fig. 1). Glacial meltwater streams flow during the austral summer through desiccated stream channels, and numerous abandoned and relict channels that do not regularly flow are also evident on the landscape. Flow extremes occur regularly and include cold and cloudy periods when flow ceases (desiccation) and episodic high flows following warm weather and sunny conditions.


Despite the short duration of highly variable flow, many Dry Valley streams harbor microbial mats in reaches with a suitably stable streambed (Alger et al. 1997). During low flow, the stream habitat is moderated by retention of meltwater through hyporheic storage (Conovitz 2000; Gooseff et al. 2003; Cozzetto et al. 2006) and the supply of nutrients and other solutes by weathering reactions in the hyporheic zone (Lyons et al. 1998; Gooseff et al. 2002). Stream temperatures are driven by diurnal changes in solar radiation ranging from 0.1 °C to over 15 °C (Cozzetto et al. 2006). Spatial variability in microbial mat type occurs across the stream width and indicates different habitat types. This study sampled the orange-colored oscillatory mats located within
the main channel (Howard-Williams et al. 1986; Vincent et al. 1993; Alger et al. 1997).

Diatoms are important phototrophs in Dry Valley microbial mats, comprising between 5% and 70% of orange algal mat biomass (Alger et al. 1997). A complete list of Antarctic stream diatom taxa and currently known distributions in the McMurdo Dry Valleys can be found in Esposito et al. (2008) and on the Antarctic Freshwater Diatoms Web site (http://huey.colorado.edu/diatoms). This detailed morphological characterization of the diatom flora of Dry Valley streams was built upon the earlier work of Kellogg et al. (1980), Round et al. (1990), and Spaulding et al. (1997). Of the 41 described species, 17 have a current distribution that does not extend beyond the Antarctic continent (Esposito et al. 2008). These endemic species are from a limited set of aeroophilic genera, primarily *Hantzschia* and *Luticola*, and are distributed throughout Dry Valley streams at high relative abundances. These two genera have the greatest number of species in the McMurdo Dry Valleys and in Antarctic freshwater environments in general (http://huey.colorado.edu/diatoms).

Microbial mat samples were collected from orange mats in seven glacial meltwater streams in Taylor Valley (Fig. 1). Sampling was conducted at long-term algal monitoring transects on Von Guerard Stream, Canada Stream, Delta Stream, Green Creek, and Bowles Creek, where the channels consist of a stable stone pavement. Canada Stream, Green Creek, and Bowles Creek drain from the Canada Glacier, and while they exhibited large differences in total annual stream flow (Table 1), all three streams received flow during every season on record (Table 2). Discharge is not continuously monitored on Bowles Creek; however, stream flow in Bowles Creek is correlated with stream flow in Green Creek (Alger et al. 1997), and flow was determined based on the relationship of manual discharge measurements between both streams as outlined by Stanish et al. (2011).

Von Guerard Stream, Delta Stream, and the Relict Channel drain alpine glaciers in the Kukri Hills and flow into the eastern side of Lake Fryxell. These are the longest streams and are characterized by a later onset of streamflow and increased hyporheic exchange. Von Guerard Stream and Delta Stream had lower total annual flows and shorter mean season length than Bowles Creek, Green Creek, and Canada Stream (Table 1). Delta Stream received flow during every season on record, while Von Guerard Stream had no recorded flow for 2 of the 20 seasons (Table 2). The Relict Channel was an abandoned channel that had not received major flow since 1969 until flow was experimentally reactivated in January 1995. Flow was diverted from the uppermost reach of Von Guerard Stream onto a dry playa area and from there into a reach of the channel with high banks (Fig. 1). A detailed description of the Relict Channel is presented in McKnight et al. (2007). Briefly, nine transects were established along the channel between 1995 and 1997 as flow reached progressively farther downstream, with the uppermost sites 1–3 receiving flow almost every season. At sites 5 and 6 the channel became narrower and steepened, and mats were abundant at site 6, but sparse at site 7 and downstream. This flow condition occurred for the next three summers, with microbial mats becoming more abundant at sites 7–9. Very low flows occurred in the summers of 1999–2000 and 2000–2001, and only sites 1–4 received flow. High flows during the summer of 2001–2002 reworked the streambed upstream of the Relict Channel and deposited large amounts of sediment on the microbial mats at the upper sites 1–3. From 2002 to 2010, flow continued to reach all sites and reached the confluence with Harnish Creek. At each site, dormant microbial mats became active shortly after receiving first flows, and the taxonomic composition of the mats resembled those found in the other streams (McKnight et al. 2007).

Wormherder Creek is in the Lake Bonney basin of Taylor Valley. Flow was first observed in the creek during the warm summer of 2001–2002 (Harris et al. 2007; Barrett et al. 2008; Simmons et al. 2009) and again during the 2005–2006 and 2008–2009 summers (Table 2). The creek was fed by glacial meltwater seepage and flowed along the western edge of a large wetland area, with another channel forming along the eastern edge. The two channels contained orange-colored
microbial mats, which were sampled at four sites in January 2009.

**Hydrologic and biological data collection**

Hydrologic, water quality, and biological data used in this study were collected as part of the MCMLTER (http://www.mcmlter.org). A stream-flow intermittency ranking was determined for each stream based on three stream-flow criteria. The first criterion, number of years when stream flow occurred for the 20 years of record (1990–2010), provided an initial ranking of streams. The second criterion, average number of flow days, was considered if the first criterion produced a tied ranking. The third criterion, average total annual discharge, was considered if the second criterion produced a tied ranking.

Microbial mat transects located on each stream were sampled as part of the MCMLTER monitoring program (Alger et al. 1997). All data included in this study were obtained after an intense flood year in 2001–2002, which scoured the streambed and altered some microbial mat diatom communities (Stanish et al. 2011). To limit the effect of habitat heterogeneity on microbial mats, only orange-colored mats from within the thalweg of the stream channel were used. Algal mat samples were analyzed from the following

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**Table 1. Discharge and biomass characteristics of streams examined in this study.**

<table>
<thead>
<tr>
<th>Stream</th>
<th>Mean total annual Q (m³)</th>
<th>Mean season duration (days)</th>
<th>Mean AFDM (mg·cm⁻²)</th>
<th>Mean chl-α (µg·cm⁻²)</th>
<th>Chl-α: AFDM</th>
<th>Algal coverage¹</th>
<th>Stream ranking</th>
</tr>
</thead>
<tbody>
<tr>
<td>Canada</td>
<td>2.06x10⁵</td>
<td>71</td>
<td>8.02 (1.09)</td>
<td>4.99 (0.93)</td>
<td>0.62</td>
<td>High</td>
<td>1</td>
</tr>
<tr>
<td>Green</td>
<td>1.42x10⁵</td>
<td>57</td>
<td>8.88 (3.74)</td>
<td>8.05 (1.58)</td>
<td>0.91</td>
<td>High</td>
<td>2</td>
</tr>
<tr>
<td>Bowles</td>
<td>2.62x10⁴*</td>
<td>57*</td>
<td>4.28 (1.05)</td>
<td>3.65 (1.82)</td>
<td>0.85</td>
<td>High</td>
<td>3</td>
</tr>
<tr>
<td>Delta</td>
<td>1.05x10⁵</td>
<td>55</td>
<td>3.93 (1.30)</td>
<td>5.16 (2.23)</td>
<td>1.31</td>
<td>Low</td>
<td>4</td>
</tr>
<tr>
<td>Von Guerard</td>
<td>5.97x10⁴</td>
<td>44</td>
<td>5.73 (1.42)</td>
<td>4.86 (2.51)</td>
<td>0.85</td>
<td>Low</td>
<td>5</td>
</tr>
<tr>
<td>Relict Channel</td>
<td>NA</td>
<td>NA</td>
<td>11.78 (1.66)</td>
<td>81.30 (12.82)</td>
<td>6.90</td>
<td>Moderate</td>
<td>6</td>
</tr>
<tr>
<td>Wormherder Creek</td>
<td>NA</td>
<td>NA</td>
<td>8.79 (3.32)</td>
<td>126.36 (25.64)</td>
<td>14.37</td>
<td>Moderate</td>
<td>7</td>
</tr>
</tbody>
</table>

Note: Values in parentheses indicate standard error. Mean total annual discharge represents the average total daily discharge measured during a summer season from 1990–1991 to 2009–2010. AFDM, ash-free dry mass; Chl-α, chlorophyll a.

*From Stanish et al. 2011.

¹See Alger et al. 1997; McKnight et al. 2007.

**Table 2. Summary of the occurrence of summer streamflow in the study streams located in Taylor Valley, McMurdo Dry Valleys, Antarctica.**

<table>
<thead>
<tr>
<th>Season</th>
<th>Canada</th>
<th>Green</th>
<th>Bowles</th>
<th>Delta</th>
<th>Von Guerard</th>
<th>Relict</th>
<th>Wormherder</th>
</tr>
</thead>
<tbody>
<tr>
<td>1990–1991</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>N</td>
<td>?</td>
</tr>
<tr>
<td>1991–1992</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>N</td>
<td>N</td>
</tr>
<tr>
<td>1992–1993</td>
<td>Y*</td>
<td>Y*</td>
<td>Y*</td>
<td>Y*</td>
<td>Y*</td>
<td>N</td>
<td>?</td>
</tr>
<tr>
<td>1993–1994</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>N</td>
<td>N</td>
</tr>
<tr>
<td>1994–1995</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>N</td>
<td>N</td>
</tr>
<tr>
<td>1995–1996</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>N</td>
</tr>
<tr>
<td>1996–1997</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>N</td>
</tr>
<tr>
<td>1997–1998</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>N</td>
</tr>
<tr>
<td>1998–1999</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>N</td>
</tr>
<tr>
<td>1999–2000</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>N</td>
<td>N</td>
<td>N</td>
</tr>
<tr>
<td>2000–2001</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>N</td>
<td>N</td>
<td>N</td>
</tr>
<tr>
<td>2001–2002</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
</tr>
<tr>
<td>2002–2003</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
</tr>
<tr>
<td>2003–2004</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>N</td>
</tr>
<tr>
<td>2004–2005</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>N</td>
</tr>
<tr>
<td>2005–2006</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
</tr>
<tr>
<td>2006–2007</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>N</td>
</tr>
<tr>
<td>2007–2008</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>N</td>
</tr>
<tr>
<td>2008–2009</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
</tr>
<tr>
<td>2009–2010</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>N</td>
<td>N</td>
<td>N</td>
</tr>
</tbody>
</table>

Total flow years 20 20 20 20 18 12 3
Stream rank 1 2 3 4 5 6 7

Note: Streamflow data are available at the MCMLTER database, with the exception of the Relict Channel and Wormherder Creek, in which flow occurrence is based on personal observations.

*Streamflow was not measured during the summer of 1992–1993. The assessment of flow occurrence was based on reports at similar locations and is supported by the rise in lake levels during the season.
seasons: 2002–2003 (Bowles, Canada, Delta, Green, and Von Guerard); 2006–2007 (Bowles, Canada, Delta, Green, and Von Guerard); and 2007–2008 (Canada, Delta, Green, Von Guerard, Relict Channel); and 2008–2009 (Relict Channel and Wormherder Creek). Surface cores of algal mats were collected using a brass cork borer (1.7 cm diameter) and placed into Whirlpack bags containing 10–15 mL stream water. One to four replicate cores were analyzed per season. Samples were preserved in 10% formalin and shipped to the University of Colorado at room temperature.

Stream water samples were collected weekly throughout the flow season for the five monitored streams and at one time point during algal mat sample collection for the Relict Channel and for Wormherder Creek. Raw water was collected in triple-rinsed 250 mL Nalgene bottles. At the field laboratory, water for nutrient analysis was filtered from the raw water sample on glass-fiber filters and frozen for later analysis. All chemistry analyses were performed at the Crary Laboratory at McMurdo Station. For the monitored streams, the mean values of all water-chemistry samples collected during a season were used in our study. Water quality values for the Relict Channel and Wormherder Creek are based on mean values obtained from all sampling sites.

Microbial mat cores were also processed for chlorophyll a (Chl-a) and ash-free dry mass (AFDM), which were analyzed at Crary Laboratory in McMurdo Station. Samples were de-watered on precombusted Whatman GF/C filters, wrapped in foil, and stored at −20 °C. Chl-a was extracted in buffered acetone and analyzed using a Turner Designs 10AU field fluorometer using the methods outlined by Welschmeyer (1994, accuracy ±10%). For AFDM analysis, samples were dried at 100 °C for 24 h, weighed, burned at 450 °C for 4 h and re-weighted, and then re-wetted and dried to determine mass loss due to hydration of sediments (accuracy ±1 mg).

Mat samples for morphological analysis were digested using heat and 30% hydrogen peroxide and rinsed several times with distilled water. A subset (~1 mL) of the digested material was dried onto cover slips and permanently mounted onto glass microscope slides with the mounting medium Zrax (refractive index = 1.7; W.P. Dailey, University of Pennsylvania, Department of Chemistry, Philadelphia, Pennsylvania). Relative abundance counts were performed using an Olympus light microscope equipped with a 1.3 NA 100× oil immersion objective under bright-field illumination, with at least 250 valves enumerated per slide. Taxonomic identifications were done according to the descriptions of Sabbe et al. (2003), Van de Vijver et al. (2004), Esposito et al. (2008), Van de Vijver and Mataloni (2008), Stanish et al. (2011), and the Antarctic Freshwater Diatoms database (http://huey.colorado.edu/diatoms). All counts data are available at the Antarctic Freshwater Diatoms Web site (http://huey.colorado.edu/diatoms). Based on the presence of chloroplasts in intact cells, 50%–77% of the diatoms were alive at the time of sampling.

Data analysis

Multivariate statistical analyses were performed using the R software package (R Development Core Team 2008). For analyses that required a distance matrix of diatom communities, rare species occurring at less than 1.0% relative abundance were removed and a distance matrix of relative abundance counts was calculated based on Bray–Curtis dissimilarity (Bray and Curtis 1957). Diatom community diversity was calculated using the Shannon index ($H'$; Shannon and Weaver 1949) using the equation

$$H' = -\sum_{i=1}^{S} (p_i \ln p_i)$$

in which $p_i$ is the relative abundance of species $i$, and $S$ is the number of species.

Evenness ($J'$) was calculated based on Pielou’s evenness for a Type A collection (Pielou 1966) using the equation

$$J' = \frac{H'}{H'_{max}}$$

in which $H'_{max}$ equals $\ln S$. Species richness was determined after removing species with a relative abundance less than 0.1%.

Nonmetric multidimensional scaling (NMDS) analyses were performed on Bray–Curtis dissimilarity matrices of square-root-transformed diatom community data using the vegan package in R. In the first ordination, the entire data set of algal mat samples was used, with the exception of samples collected from the Relict Channel prior to 2001. A three-dimensional model produced a goodness of fit value of 7.8% based on Kruskal’s “stress” (Faith et al. 1987). A Shepard plot of calculated versus raw dissimilarities showed a strong nonmetric ($r^2 = 0.99$) and linear fit ($r^2 = 0.97$). In the second ordination, Relict Channel samples collected at the start of the flow reactivation experiment in January 1995 were included with the Relict Channel samples collected during the 2008–2009 and 2009–2010 seasons. A three-dimensional model produced a Kruskal’s stress value of 0.10, with a non-metric and linear fit of 0.99 and 0.93, respectively.

Hierarchical cluster analysis was performed on diatom community data with a sample distance matrix generated using Bray–Curtis dissimilarity. The clustering method that produced a classification tree with the highest cophenetic correlation coefficient (which describes the similarity of the modeled distances to the original pairwise distances) was used. Based on this criterion, the average linkage method was chosen (coeff = 0.89).

Results

Stream-wide variation in hydrologic conditions and microbial mats

The first criterion for ranking the intermittency of flow regime, the number of summer seasons in which flow occurred, resulted in a ranking of the three streams at the highly intermittent end of the gradient (Table 2). The occurrence of flow in Wormherder Creek in only three of the 20 years of record placed this stream at the most intermittent end of the gradient, followed by the Relict Channel with flow occurring during 12 years and Von Guerard Stream with flow occurring during 18 years. The other streams, Canada Stream, Green Creek, Bowles Creek, and Delta Stream, have experienced some flow at the transect site every season since 1990. The second criterion, average duration of flow, corresponds to the season for microbial mat growth. Canada Stream was at the least in-
termittent end of the gradient, with an average flow season length of 77 days (Table 1). Delta Stream had a higher altitude source glacier and a longer stream reach, which delayed melt and the arrival of flow at the transect site and therefore reduced the duration of the flow season. Green Creek and Bowles Creek drained the same pond system at the base of the Canada Glacier, and it was assumed that they had the same average flow duration. The third criterion is average total annual discharge (Table 1), which represents the extent to which streams with lower average flows may have areas of the streambed that become dry even when there is still some flow. Application of this criterion resulted in a ranking of Bowles Creek as more intermittent than Green Creek.

Consistent with observations made before the flood event (McKnight et al. 2004), analysis of nutrient data after the flood event showed that streams with low to moderate algal coverage (Table 1) had significantly higher PO₄ concentrations than streams with high algal mat coverage (analysis of variance, ANOVA, p < 0.0001, Table 3). NO₃ concentrations were similar across all streams with the exception of Wormherder Creek, which had nearly 10 times higher NO₃ than the other streams (ANOVA, p < 0.0001, Table 3). Stream nutrient concentrations also varied considerably within and across seasons, as indicated by the large standard deviations (Table 3).

The AFDM and Chl-α content of the microbial mats provides information about the potential differences in the cyanobacterial mat matrix in which the diatoms grow. Both of these parameters vary approximately twofold at a transect site during the same summer, reflecting patchiness in the mat distribution with flow (data not shown), similar to previous observations (http://mcmlter.org). In general, the threefold range in AFDM across the flow intermittency gradient, from 3.93 mg·cm⁻² at the Delta Stream site to 11.78 mg·cm⁻² in the Relict Channel, was only somewhat greater than the twofold reach-scale variation in AFDM. By contrast, the Chl-α content was much higher in the microbial mats in the most intermittent streams. For example, the mats in Wormherder Creek had Chl-α contents that were about 50-fold greater than the mats in Canada Stream. Given that the AFDM values are similar, this difference results in an autotrophic index (Chl-α:AFDM) that is also much higher in Wormherder Creek.

**Stream-wide variation in diatom community composition**

Microbial mat diatom species are represented ubiquitously across streams, with many species being present in most streams (Fig. 2). Thus, species turnover across Dry Valley stream microbial mats is generally low. However, the dominant species within a stream changes progressively (Fig. 2). When the streams are considered along a gradient of increasingly infrequent summer flow, a pattern in the importance of different species emerges. For example, *Psammothidium* sp. #1 and species of the genus *Luticola* occurred abundantly in the least intermittent streams, Canada Stream and Green Creek, but were rare or absent from Wormherder Creek, the most intermittent stream. Similarly, two of the five species of *Luticola* that dominated the diatom flora in Wormherder Creek were rare or absent in Canada Stream and Green Creek.

There was a decrease in species richness with increasing flow intermittency. Diatom community diversity had a unimodal relationship with flow ranking, with intermediate ranked streams having the highest Shannon index of diversity (*H′*, Fig. 3a). Similarly, a peak in *H′* was observed when the relative abundance of *Luticola* species was between 30% and 50% (Fig. 3b). Differences in the underlying community structure were apparent when comparing the relationship between *H′* and species richness or evenness for each stream. In the lowest ranked Canada Stream, which flowed every year and had the most consistent stream flow, the relationship between *H′* and diversity differed from the other streams in that *H′* was much lower for the same richness value (Fig. 3c). However, the relationship between *H′* and evenness in Canada Stream had a strong linear fit with the other streams (*r² = 0.92, Fig. 3d). By contrast, the most intermittent stream, Wormherder Creek, did not show a strong correlation between *H′* and evenness (*r² = 0.39, Fig. 3d). Because the relationship between *H′* and richness plateaus at high richness values (DeJong 1975), Simpson’s diversity was also determined and similar relationships were observed (data not shown).

The two most species-rich Dry Valley diatom genera, *Luticola* and *Hantzschia*, had relative abundances that responded differently to the flow intermittency ranking (Figs. 2 and 4). Nearly half of the diatoms counted in Bowles Creek belonged to the genus *Hantzschia*, which was significantly higher than all other streams except Von Guerard Stream. Along the flow intermittency gradient, *Hantzschia* abundances peaked in streams with more moderate flow frequencies (Fig. 4). There was an increase in the relative abundance of *Luticola* species with increasingly intermittent flow (*r² = 0.75, p < 0.0001, Fig. 4), with 90% of diatoms counted in Wormherder Creek belonging to the genus *Luticola*.

These patterns at the genus level were found to be composed of different patterns (unimodal, bimodal, and monotonically) for the species within the genus, which can be seen by scaling the relative abundance of a taxon to the total relative...
abundance of the genus (Figs. 5 and 6). Within the genus *Hantzschia*, the cosmopolitan species *H. amphioxys* was an important representative in all streams ranging from 25% to 55% of the total *Hantzschia* count (Fig. 5). The other cosmopolitan species, *H. abundans*, was less abundant in Canada Stream and Green Creek than in the other streams. The endemic species showed greater variation in distribution across the flow intermittency gradient. One of the endemics, *H. muell-*
The effects of interannual variation in flow intermittency

Diatom community variation in the Relict Channel

The effects of interannual variation in flow intermittency

counting for ~10%–30% and ~5%–30%, respectively, of the Luticola count (Fig. 6). The other abundant cosmopolitan species, L. muticopsis, decreased in the more intermittent streams. Among the endemic species, responses were also varied. A uniform distribution was exhibited by L. australatlantica and L. laeta, whereas L. dolia reached three times higher relative abundance in the highly intermittent Wormherder Creek.

NMDS results showed a clear clustering of diatom communities by stream (Fig. 7a). Along NMDS axis 1, the streams were arranged in order of the flow intermittency ranking, with Canada Stream lying farthest to the left and Wormherder Creek lying farthest to the right. There was a significant difference in diatom communities across all streams, as well as significant pairwise distances between all streams (permutational multivariate analysis of variance (PERMANOVA, Anderson 2001), p < 0.05).

Along NMDS axis 1, samples separated based on the relative abundances of Psammothidium sp. #1 and Diadesmis spp. on the left versus Luticola species on the right (Fig. 7b). Variation along the second axis was driven by changes in the relative abundance of Fistulifera pelliculosa, which reached high relative abundances in the Relict Channel and in certain samples from Delta Stream and Von Guerard Stream (Fig. 7b). Members of the genus Luticola separated along a gradient on both axes 1 and 2.

Fig. 3. Shannon index of diversity (H') versus (a) flow intermittency ranking; (b) percent Luticola per sample; (c) species richness; and (d) evenness. In panels (c) and (d), closed circles represent Canada Stream, open circles represent Wormherder Creek, and triangles represent other streams.

Fig. 4. Total mean relative abundances of the genera (a) Hantzschia (black bars) and (b) Luticola (gray bars) plotted along the flow frequency gradient. Streams are ordered by flow intermittency ranking. Error bars show standard error.

leri, decreased and another, H. subrupestris, increased along the gradient of increasing intermittency (Fig. 5).

Within the genus Luticola, each taxon showed a distinctive relationship with flow intermittency. The cosmopolitan taxon L. mutica and the endemic taxon L. australatlantica showed relatively uniform distributions across the study streams, accounting for ~10%–30% and ~5%–30%, respectively, of the Luticola count (Fig. 6). The other abundant cosmopolitan species, L. muticopsis, decreased in the more intermittent streams. Among the endemic species, responses were also varied. A uniform distribution was exhibited by L. australatlantica and L. laeta, whereas L. dolia reached three times higher relative abundance in the highly intermittent Wormherder Creek.
on diatom communities were examined in the Relict Channel, in which longitudinal data were available along the stream length. Diatom communities from nine sites were compared during a low flow summer (2007–2008), a high flow summer (2008–2009), and with samples collected immediately after channel reactivation in 1995. Hierarchical cluster analysis showed that the samples collected in 1995 clustered together (Fig. 8). Among the samples from the two later summers, diatom communities separated into four clusters. Samples collected at the uppermost sites 1 and 2 were more similar in both 2008 and 2009 than to downstream sites sampled during the same season. One cluster contained data for sites 6 and 9, which are fed by seepage water and may have a steadier source of water than the other sites. The fourth cluster contained samples primarily from site 3. The three sets of duplicate samples collected from the same sites during the low flow summer of 2007–2008 also clustered together, suggesting that the intrasite variation in diatom community composition was less than the intersite or temporal variation. Overall, the cluster analysis suggests that intersite variation influenced diatom communities more than temporal variation in the Relict Channel.

NMDS results showed a clear difference in diatom community composition from samples collected immediately following channel reactivation and samples collected more than a decade later, with samples collected in 1995 forming a separate cluster from those collected in 2008 and 2009 (Fig. 9). This temporal variation was apparent along NMDS axis 1 and was driven by increases in the relative abundances of Fistulifera pelliculosa, Mayamaea atomus, and M. atomus v. #1, which were rarely observed in the 1995 samples (Fig. 9). Fistulifera pelliculosa was also less abundant during the high flow summer of 2009 than during the low flow summer of 2008 ($p < 0.01$). In contrast with the ordination results from the multistream data set (Fig. 7), Luticola species in the Relict Channel NMDS were mostly positioned at the center of both axes (Fig. 9). Luticola dolia was more abundant in the 1995 samples, and it was an important driver of variation in diatom communities in the larger data set (Fig. 7b). Species of the genus Hantzschia separated along NMDS axis 2, with H. subrupestris positioned at the upper end, Hantzschia sp. #5 at the lower end, and the two cosmopolitan species, H. amphioxys and H. abundans, in the center.

Discussion

The McMurdo Dry Valleys are unique habitats in which to study fundamental ecological processes because of the relatively simple ecosystems and lack of anthropogenic inputs. In these habitats, the availability of water is a pervasive limit to microbial growth. As a result, there is potential to examine fundamental relationships between flow regimes and benthic diatom community structure that can be useful to understand more complex ecosystems that experience intermittent flow. The frequency of summer flow may be considered an environmental filter that, according to Poff (1997) and others (e.g., Belyea and Lancaster 1999), allows certain members of the available species pool to pass. Based on this definition, flow intermittency appears to be a strong environmental filter that limits the establishment of diatom species in the microbial mats in certain Dry Valley streams. First, there are ob-

![Fig. 5. Mean relative abundances of representative species within Hantzschia plotted from lowest to highest flow intermittency. Error bars show standard error.](image-url)
vious changes in the relative importance of diatom species and genera in microbial mats across the gradient in flow frequency. In addition, as demonstrated in Fig. 2, species turnover is low across the Dry Valley landscape, suggesting that differences in species composition are not due to dispersal limitation.

Most Antarctic stream diatoms belong to genera containing known aerophiles. Considering that the ability to survive extended periods of desiccation is a requirement for persisting in the perennial mats of Dry Valley streams, other traits in addition to desiccation tolerance may contribute to the observed shifts in species dominance. For example, our results show that the microbial mats living under the most intermittent flow regime have the highest autotrophic index, indicating a lack of biomass accumulation resulting from shorter and less frequent growth periods. This result mirrors the autotrophic index of the Relict Channel, which also exhibited greater algal mat growth rates than the neighboring, regularly

Fig. 6. Mean relative abundances of representative species within *Luticola* plotted from lowest to highest flow intermittency. Error bars show standard error.
Fig. 7. Nonmetric multidimensional scaling plot of Bray–Curtis dissimilarities for diatom communities from all streams. (a) Ordination results displaying sample coordinates. Streams are indicated by the first letter of the stream name. (b) Species with relative abundances > 5% displayed at their centers of distributions. Key to species abbreviations: Ataylor, Achnanthes taylorensis; Ampholig, Amphora oligotraphenta; Cmolest, Craticula molestiformis; Dcontp, Diadesmis contenta v. parallela; Dcont, D. contenta; Dperp, D. perpusilla; Fpellic, Fistulifera pelliculosa; Hantsp, unidentified Hantzschia; Habun, H. abundans; Hanne, H. amphioxys; Hantsp5, Hantzschia sp. #5; Hsubru, H. subrupes-tris; Hmuell, H. amphioxys f. muelleri; Ldol, Luticola dolia; Llaeta, L. laeta; Lmuta, L. mutica; Lmutcop, L. muticopsis; Lrede, L. muticopsis f. reducta; Ls23, Luticola spp. #2–3; Matomus, Mayamaea atomus; Matomusv1, Mayamaea atomus v. #1; Muellsp, unidentified Muelleria; Mperaus, Muellera perauralis; Msupra, Muelleria suprarentaria; Nshac, Navicula shackletoni; Pboor, Pinnularia borealis; Pdeltaica, Pinnularia deltaica; Pquat, Pinnularia quaternaria; Pgerm, Psammothidium germannii; Psp1, Psammothidium sp. #1; Slatis, Stauroneis latistauros.

Hantzschia is the second most diverse genus and is known to have highly mobile taxa that prefer moist or intermittently wetted habitats common in low flow streams (Round et al. 1990). Consistent with these observations, in Dry Valley streams, Hantzschia species peak in the lower flow habitats found in Bowles Creek, Delta Stream, and Von Guerard Stream. A similar clustering of Hantzschia species in lower flow streams has been previously observed (Stanish et al. 2011) and suggests a common adaptation of the genus to similar environmental conditions. The decrease in the relative abundances of Hantzschia species in the most intermittent streams suggests that this genus is better adapted to low flow habitats that have a consistent supply of water.

The importance of species evenness in driving community composition has received more attention recently with regards to its importance on ecosystem function (Hillebrand et al. 2008). The unimodal relationship between diatom diversity and the ranking of stream flow intermittency, which was also observed in relative abundance counts of the genus Luticola, have been shown in other studies (Li 2002; Esposito et al. 2006). However, our results also suggest that flow intermittency may influence species evenness, thereby affecting ecological processes. The finding that the most species-poor stream, Wormherder Creek, has similar Shannon index values as the species-rich Canada Stream suggests that factors affecting species dominance, such as competitive exclusion, may play a pivotal role in structuring the diatom commun-
ities in Canada Stream. Wormherder Creek, on the other hand, appears to have a less competitive environment in which a single taxon (i.e., species trait(s)) is less likely to become dominant.

The ordination analysis reveals interesting patterns in diatom species distribution that could potentially be used to infer flow regime in other Dry Valley streams that are not monitored. Stream-scale characteristics clearly structure diatom communities, which is evident by the distinct clustering of samples by stream. For example, Delta Stream, which flowed every year since 1990, clustered more closely with the less frequently flowing streams, Von Guerard Stream and the Relict Channel, than with streams experiencing more similar flow regimes, such as Canada Stream and Bowles Creek. Stream length is most likely the underlying explanatory factor because not only is the duration of stream flow shorter, but stream flow also arrives later at the sample site, which is located at the lake outlet. Longer streams also exhibit much larger variation in stream flow between seasons (Stanish et al. 2011). Given these findings, we believe that diatom community composition strongly reflects larger landscape features and may provide testable hypotheses about flow patterns in ungauged streams.

The importance of Fistulifera pelliculosa along NMDS axis 2 is surprising given that this species is relatively rare in Dry Valley microbial mats. Fistulifera pelliculosa is a small, lightly silicified diatom that has been found in the phytoplankton and the epilithon (Perez et al. 2009; Morales et al. 2009). In the Dry Valleys, it may reside in upstream ponds and playas and be mobilized during high flow events and deposited on algal mats. The significant decrease in the relative abundance of F. pelliculosa in the Relict Channel between 2008 and 2009 suggests that high flows mobilized this species and further supports this conclusion. Interestingly, there was a complete lack of F. pelliculosa in algal mats collected at the start of the channel reactivation experiment in 1995, suggesting that the resumption of flow to the channel opened up new habitat for this species. The interannual variation in the Relict Channel may therefore reflect community variation that is not driven only by the conditions in the microbial mats themselves, but rather by landscape changes.

These results have implications for stream ecosystem responses to future climate changes in the Antarctic. By understanding the autecology of species with regard to their ability to withstand long periods of desiccation, we can better predict potential changes to diatom biodiversity as stream habi-
tats change. Under a warmer Antarctic climate with increasing occurrence and duration of stream flow (Turner et al. 2009), the Dry Valley streams currently studied in Taylor Valley may become less suitable for species that are well adapted to extremes in water availability, thereby lowering the selective advantage for certain genera, particularly Luti-
cola. Many of these species are endemic to Antarctica, implying that stream habitats promoting species radiation may be displaced inland and to higher elevation as warming conditions occur and other abandoned and relict channels are reactivated. As current stream habitats evolve, new stream habitats are likely to emerge and may serve as refugia for desiccation-adapted, endemic species.

Acknowledgements

This analysis was carried out on samples collected by many researchers affiliated with the MCMLTER over the past two decades. Funding was generously provided by the MCMLTER (OPP-9211773, OPP-9810219, OPP-0096250) and NSF Antarctic Organisms and Ecosystems Program Award No. 0839020. Raytheon Polar Services Company and PHI Helicopters provided essential logistic and transportation support during field campaigns.

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