



Spatial and temporal patterns of microbial mats and associated invertebrates along an Antarctic stream

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Abstract

Microbial biofilms are biological hotspots in many alpine and polar ecosystems, but the controls on and functional significance of their fauna are little known. We studied cyanobacterial mats and the underlying sediment in a glacial meltwater stream in the McMurdo Dry valleys, Antarctica. We investigated mat biomass (total and phototrophic), diatoms, and micro-meiofauna (nematodes, rotifers, and tardigrades) at nine sites along a 1670 m stream reach in a cold, low-flow growing season, and in a warmer growing season in which peak flows (above 100 L s⁻¹) scoured the mats. Diatom and invertebrate communities were not related, but mat biomass in the low-flow year was negatively related to nematode abundance, including that of the omnivore *Eudorylaimus*. In the high flow year that followed, invertebrate abundance was reduced in the mats, diatom community structure was altered, and mat biomass was higher. The difference in invertebrate abundance between years was greater in mats in upstream reaches, where the greatest increases in flow velocity may have occurred, and was negligible in mats in downstream reaches as well as in the sediment beneath the mats. Integrating our results with previous findings, we generate two predictive hypotheses to be tested in glacial meltwater streams: (1) under peak flows invertebrates decline in the microbial mats, while (2) the sediment beneath the mats is a refuge from the flow disturbance. Our results also suggest that, under stable flow conditions, microinvertebrate grazers could exert top-down control on microbial mat biomass.

Keywords Diatoms · Disturbance · Dry valleys · Epilithon · Microfauna · Streamflow

Introduction

Microbial biofilms are found in many freshwater and aquatic-terrestrial interfaces, as well as in thermal springs, intertidal flats, and on land as biological soil crusts (Grimm and Petrone 1997; Paerl et al. 2000; Rott et al. 2006; Zakhia et al. 2008). They have a disproportionately large role on freshwater ecosystem functioning, modulated by hydrological conditions and grazing invertebrates (Battin et al. 2003; Hillebrand 2009). At high latitudes, mats dominated by filamentous cyanobacteria are often the most important contributors to biomass and primary productivity (Paerl et al. 2000; Vincent and Quesada 2012). These biostructures host micro-meiofauna such as nematodes, rotifers, and tardigrades, the role of which in the benthic food web has so far been investigated in temperate streams (Schmid-Araya et al. 2008; Majdi et al. 2012), but not at high latitudes. Ecological studies on microbial biofilm fauna at high latitudes have been particularly sparse to date, despite the fact that microscopic invertebrates

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constitute the highest trophic level in some of those ecosystems (Vincent and James 1996).

In this study, we investigated the invertebrates (nematodes, rotifers, and tardigrades) and diatoms in stream microbial mats in the McMurdo dry valleys (MDVs), Antarctica. MDV streams flow only for max 12 weeks per year (late November–February), fed by melting of the glaciers that surround these hyper-arid valleys. Main features of these ephemeral streams were reviewed by McKnight et al. (1999), and include: relatively unstable banks devoid of vegetation (save for rare moss patches); a shallow active layer above the permafrost (approx. 0.5 m beneath the surface); a wide hyporheic zone; considerable interannual and daily variability in streamflow (up to tenfold variation in a single day); and perennial cyanobacterial mats that overwinter in a freeze-dried state and rapidly reactivate when water flow resumes (McKnight et al. 2007). These mats exhibit four distinct morphologies with different microbial taxonomic composition and different habitats within a stream reach, principally orange mats dominated by Oscillatoriales in conditions of flowing water, and black mats dominated by Nostocales along stream margins (Stanish et al. 2011). These mats are biotic (McKnight et al. 1999; Niederberger et al. 2015) and geochemical (Barrett et al. 2009) hotspots in a polar desert which lacks vascular plants and macroscopic animals, and receive almost no terrestrial detritus input (Adams et al. 2006).

Although the MDVs lack insects, crustaceans, or vertebrates, the mats may support high abundance of rotifers, tardigrades, and nematodes (Cathey et al. 1981; Simmons et al. 2009; Smykla et al. 2012; Iakovenko et al. 2015). In contrast to a rich ecological literature on the microbes and algae in MDV and other polar microbial biofilms (Vincent and James 1996; Varin et al. 2010; Jungblut et al. 2012; Stanish et al. 2013; Cavicchioli 2015), the ecology of the corresponding fauna is less studied (Rautio and Vincent 2006; Simmons et al. 2009). Long-term studies have shown that MDV mat biomass and diatom communities are strongly controlled by interannual streamflow variation (Kohler et al. 2015b), with significant scouring occurring at peak flows above 100 L s^{-1} (Esposito et al. 2006; Cullis et al. 2014), but how the invertebrates respond to such streamflow variation is not known. The functional significance of microbe-animal interactions in MDV streams is also unclear. Although it has been suggested that micro-meiofauna in polar ecosystems has negligible top-down effects on microbes and microalgae (Vincent and Quesada 2012), so far evidence is limited to some Arctic food webs (Rautio and Vincent 2006). Biotic interactions in MDV soils are relatively weak (Hogg et al. 2006), with communities mostly shaped in response to abiotic stresses (Magalhães et al. 2012), but whether trophic interactions are stronger in the mats is untested. As such,

it is not known whether MDV invertebrates exert top-down effects on microbial mat biomass in field conditions.

In this study, we investigated patterns in diatom and invertebrate communities along a glacial meltwater stream in Taylor valley, Antarctica. The stream was reactivated by a flow diversion in 1995 after two decades of hydrological inactivity. Abundant cyanobacterial mats, dominated by *Phormidium* and *Oscillatoria*, reactivated within a week and remained highly productive (relative to local standards) through the following years (McKnight et al. 2007). Building on these earlier findings, a decade after reactivation (Kohler et al. 2015b), we surveyed diatoms and invertebrates in two growing seasons with contrasting streamflow intensity, one of which was characterized by scouring flows (above 100 L s^{-1}). Invertebrates were also surveyed from the underlying sediment, where they might influence nutrient cycling and thus indirectly affect the mats. Here we describe how patterns in microbial mat biomass, diatoms, and microinvertebrates varied in relation to each other and to physico-chemical properties (nutrient content, depth to permafrost, and conductivity) in the two sampling years. Our aim with these observational data was to generate predictive hypotheses on the controls on and functional significance of microbial mat invertebrate communities in Antarctic glacial meltwater streams and similar ecosystems. In particular, we followed two exploratory hypotheses. First, given our understanding of the role of interannual streamflow variation in controlling microbial mats in the dry valleys, we expected mat biomass, and invertebrate abundance and diversity to be reduced in the high flow year. Second, as biotic interactions in the dry valleys are thought to be weak (Hogg et al. 2006), we expected no link between invertebrate abundance and mat biomass or diatom community composition.

Materials and methods

Study site

The study was performed in the McMurdo dry valleys, Antarctica (MDVs), in Taylor valley, the remote polar desert site of the NSF Long Term Ecological Research network (<http://mcm.lternet.edu>). Streams in the MDVs flow for a maximum 12 weeks per year during austral summer, and due to the lack of vascular plants in the surrounding valleys they receive negligible inputs of terrestrial detritus. In January 1995, a 2-km-long channel in the Fryxell Basin, Taylor valley, was experimentally reactivated after at least 20 years of inactivity. A low sandbag wall, filled with local alluvium, was used to divert streamflow from an upper creek, Von Guerard Stream, with minimal alteration of water quality. McKnight et al. (2007) describe the operation and report the rapid recovery of cyanobacterial mats after flow reactivation

in the first two years. For the present study, orange-coloured mats were sampled within the reactivated stream channel on 18 January 2008 and 7 January 2009, during the peak of the short MDV growing season.

Flow data

Year 1 (summer 2007–2008) was colder than Year 2 (summer 2008–2009), and this influenced flow regime, as evidenced by stream flow measurements from a gauge at a control site on Von Guerard Stream near the outlet to Lake Fryxell (Fig. 1). The headwater reach of Von Guerard Streams is the source of the diverted streamflow (Table 1 and Online Resources 1). Flow data in Von Guerard Stream indicate that total and maximum flows were much higher in the second year of sampling, with total flow over 10 times larger than in the first year (Table 1). Maximum flow exceeded 100 L s^{-1} only rarely and by a small margin in Year 1, whereas it did so frequently and by a wide margin (up to 4.5-fold) in Year 2 (Table 1 and Online Resources 1). Similarly, the instream flow velocities measured on dates near the dates of maximum flows were much higher in the second year (Table 1 and Online Resources 1). More importantly for this study, the average channel velocity of 0.46 m s^{-1} for the high flow on 17/12/2007 was slightly below of the range of velocities found to initiate scour in sand-silt streambeds [0.55 to 0.88 m s^{-1} , Hughes (1980)]. In contrast, the average channel velocity 1–2 days after the dates of maximum flow in the second year, 1.22 m s^{-1} , exceeded this range, indicating the occurrence of scouring conditions in the main channel. In addition, the velocities at the time of the maximum flow would have likely been higher. Because the study stream received a lesser portion of the flow above the diversion than lower Von Guerard Stream, its total and maximum flows were lower than those recorded at the gauge site at the lake outlet. In particular, the flow in the study stream at the time of sampling in January 2009 was likely below the 110.6 L s^{-1} measured in Von Guerard Stream. It is also unlikely that in Year 1 the study stream received flows exceeding 100 L s^{-1} . Because the study stream is similar in width to Von Guerard Stream, the differences in flow velocities between the 2 years would likely have been similar to those in Von Guerard Stream.

Sampling

Sampling occurred 29 days after the peak flow in Year 1 and 10 days after the peak flow in Year 2 (Table 1) at $n=9$ locations along the stream reach (Fig. 1), starting below the diversion wall ($77^{\circ}37'55''\text{S}$, $163^{\circ}17'52''\text{E}$) and ending 1670 m downstream ($77^{\circ}37'13''\text{S}$, $163^{\circ}15'46''\text{E}$). The sampling locations were chosen to roughly correspond with the original locations, which were indicated by cairns near

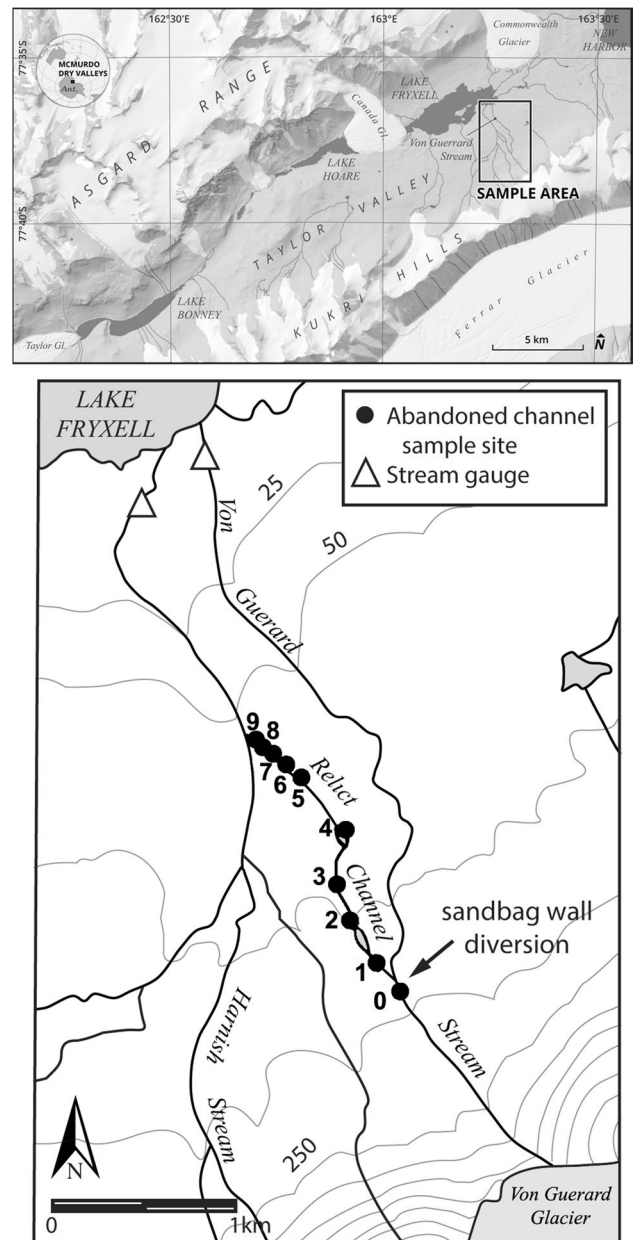


Fig. 1 Top: location of the study region in the McMurdo dry valleys, Victoria Land, Antarctica (map by Brad Herried, Polar Geospatial Center). Bottom: map of Von Guerard Stream, Harnish Creek and the reactivated channels in which samples were collected

the stream margin from the initial study by McKnight et al. (2007). Below the area of the diversion, the stream follows a distinct route through an extensive relatively flat area for sites 1–4. Although the stream banks are not well defined, this route has hardly changed since the initial diversion. During cold summers when there is little meltwater generated from the glacier, small terminal ponds sometimes form in the reach between sites 1 and 2 and near site 4, and flow does not reach the lower channel, where sites 5–9 are located. This

Table 1 Mean air temperature of Taylor valley (December–February, meteorological station at Lake Hoare) and stream flow in the Von Guerard Stream, i.e. the upper stream from which water was diverted into the study stream, in the two sampling seasons

	Year 1	Year 2
Entire season characteristics		
Air temperature (°C)	− 4.6	− 5.3
Total flow ($\times 10^3 \text{ m}^3$)	18.1	194.2
Start–end dates	16/12/2007–03/02/2008	12/12/2008–07/02/2009
Duration (days)	49.7	56.9
Max flow (L s^{-1})	110.6	462.9
Max flow dates	17/12/2007, 20/12/2007	28/12/2008, 29/12/2008
Measured high flow velocities, channel average (m s^{-1})	0.46	1.22
Measured high flow dates	17/12/2007	30/12/2008
At the time of sampling		
Sampling date	18/01/2008	07/01/2009
Max flow (L s^{-1})	26.3	110.6
Date of prior flow $> 100 \text{ L s}^{-1}$	20/12/2007	Not applicable
Days since flow $> 100 \text{ L s}^{-1}$	29.03	Not applicable

Flow days indicate the number of days in which positive flow was recorded. Measurements are from a gauge located about 100 m from the stream mouth, near Lake Fryxell, and were taken at 15 min intervals during the flow season since 1990 (<http://mcm.lternet.edu>). For daily flow during the two sampling seasons and cumulative annual flow since 1990–1991, see Online Resources 1. Note that total and max flows along the study reach were lower than in Von Guerard Stream

lower channel has a steeper gradient than the flat area, high banks (about 2 m high), and a channel that ranges from 5 to 15 m in width. Sites 5–9 have similar characteristics, but the lower sites may experience flow for shorter periods during cold summers when the flow does reach the lower channel, as described by McKnight et al. (2007). For all sites, orange mats dominated by species of *Phormidium* and *Oscillatoria* (McKnight et al. 2007) are abundant in the main channel. The orange mats are typically cohesive and often have a rubbery texture. Black mats dominated by species of *Nostoc* are present at the stream margin. In the lower channel, patches of moss occur in some areas above the black mats. For this study, orange mats near the thalweg were sampled.

Samples in Year 2 were located a few metres from those taken in the first year, to ensure that they were not affected by the disturbance of the previous sampling event. The number of sampling locations was deemed appropriate to the short length of MDV streams (only a few km); greater replication would have been problematic due to the logistical challenges of performing field work in this remote site with a short growing season. At each of nine sampling locations per year, the following procedure was followed: (1) a water sample was taken to measure water quality parameters following standard LTER protocols (Online Resources 2); (2) four microbial mat sub-samples were collected using a clean #13 brass cork borer and placed into a sterile Whirlpak bag with ~10 ml stream water, and then preserved with formalin (5% final volume); (3) another mat sample and 500 g of sediment from directly underneath were taken using sterile scoops and placed into sterile Whirlpak bags.

Laboratory analyses

Within 48 h after sampling, invertebrates were extracted from mats (average 6.2 g dry weight per sample) and sediment (approx. 100 g in Year 1 and 50 g in Year 2, per sample) under a sterile laminar flow hood using a sugar-centrifugation technique developed for MDV soil (Freckman and Virginia 1993). Animals were enumerated under light microscopy, distinguishing tardigrades, rotifers, and nematodes. A single morphospecies was found for tardigrades (*Acutuncus antarcticus*) and rotifers (unidentified). The nematodes were further identified to species (*Plectus frigophilus* and *Eudorylaimus* sp.), sex of *Eudorylaimus* sp. (males of *P. frigophilus* are extremely rare), and life stage. The taxon we refer to as *Eudorylaimus* sp. resembles *E. sextus* and *E. nudicaudatus*, but is likely a new species, and is clearly different from *E. antarcticus*. Total mat biomass was quantified as ash-free dry mass (henceforth AFDM), and chlorophyll *a* content was used as a complementary indicator of phototrophic biomass, measured following MCM LTER protocols (Online Resources 2). The ratio of chlorophyll *a* to AFDM was used as an indicator of photosynthetic activity, with greater ratios pointing to higher photosynthetic activity (McKnight et al. 2007).

Diatom preparation and analysis

Microbial mat samples were processed according to the methods outlined in Stanish et al. (2013). Relative abundances were determined by counting a representative

number of diatom valves, with taxonomic identifications based on Sabbe et al. (2003), Vijver et al. (2004), Esposito et al. (2008), and Kohler et al. (2015a). To simplify comparison with the physico-chemical and animal data, the four sub-samples per each sampling point were averaged.

Statistical analyses

Diversity of diatoms (species) and that of invertebrates (four morphospecies: tardigrades, rotifers, *P. frigophilus*, *Eudorylaimus* sp.) were quantified as Shannon index and Pielou's evenness index. To explore patterns in community structure, non-metric multidimensional scaling ordination (NMDS) was performed on Bray–Curtis dissimilarity matrices of mat and water properties available in both years (AFDM, chlorophyll *a*, NO₃, PO₄ and permafrost depth), diatom species, and invertebrate taxa. Non-parametric multivariate analyses of variance (npMANOVA, 999 random permutations) were performed on each matrix to test whether year explained community patterns; for invertebrates, npMANOVA also included microhabitat (mat vs sediment) and its interaction with year, and was stratified by location along the stream to account for the non-independence of a given mat and the sediment underneath. Mat samples from a given location in Year 1 and Year 2 were not considered repeated measurements on the same statistical sample because they were spatially distinct.

Mann–Whitney *U*-tests were used to test whether physico-chemical and biological properties, diversity measures of diatoms and invertebrates, and abundance of invertebrates (in total and for each taxon) differed significantly between years ($n = 9$ locations $\times 2$ microhabitats $\times 2$ years). Spearman's correlations were calculated between mat and water properties and invertebrate abundances (total and for each taxon), between diatom and mat invertebrate diversity, and between diatom diversity and mat invertebrate abundance, separately by year. Linear mixed-effect models with location as random effect and year, microhabitat and their interaction as fixed effects were used to test how invertebrate abundances and diversity differed between microhabitats and years; if the interaction was significant, microhabitats in each year were compared with paired Mann–Whitney *U*-tests. Linear regression models were used to test whether location, i.e. distance downstream from the flow diversion wall, explained variation in environmental and biotic variables, separately by year; based on differences in physical conditions between the upper and the lower sampling sites above described (see “Sampling”), we expected invertebrate abundance to decrease downstream. Analyses were performed in R 3.1.3 (R Core Team 2016), using libraries *vegan* for the multivariate analyses (Oksanen et al. 2015) and *nlme* for the mixed-effect models (Pinheiro et al. 2014). Model assumptions were confirmed by visual inspection of

the residuals (Zuur et al. 2010), and invertebrate abundance data were log-transformed as $\ln(x + 1)$. Unless otherwise specified, data are shown as mean $\pm$ standard error.

Results

Physico-chemical and biological properties

NMDS ordination on the physico-chemical and biological properties available in both years failed to show a clear year effect, as confirmed by npMANOVA ($p > 0.10$, $R^2 = 0.06$). However, univariate analyses revealed that AFDM, chlorophyll *a* and permafrost depth were all significantly higher in Year 2 (Table 2). The ratio of chlorophyll *a* to AFDM did not vary significantly between years (Table 2), indicating comparable levels of photosynthetic activity in both years. These ratios were similar to those found shortly after the diversion a decade previously and are at the high end of the range for mats in MDV streams. In Year 2, permafrost depth also increased downstream ($F_{1,7} = 7.22$, $p = 0.03$), while no spatial pattern was found in Year 1, or for the other measured properties. However, when location along the stream and its interaction with year were included in the npMANOVA, a significant interaction was found explaining 25% of the variance in physico-chemical and biological properties ($p = 0.006$, $R^2 = 0.25$). In fact, downstream PO₄ and NO₃ concentrations were considerably higher in Year 1, whereas upstream, they were higher in Year 2 (Online Resources 2).

Diatom community composition and diversity

Location along the stream and physico-chemical properties did not explain significant patterns in diatom diversity,

Table 2 Physico-chemical and biological properties of microbial mats and water column in a reactivated stream in Taylor valley, Antarctica (mean $\pm$ SE, $n = 9$ per year)

Measurement	Year 1	Year 2	<i>p</i> value
AFDM (mg cm ⁻²)	9.12 $\pm$ 1.84	15.30 $\pm$ 2.06	0.05
Chlorophyll <i>a</i> (µg cm ⁻²)	10.52 $\pm$ 3.19	17.98 $\pm$ 1.95	0.02
Chlorophyll <i>a</i> : AFDM (ratio)	1.03 $\pm$ 0.20	1.29 $\pm$ 0.14	0.37
DOC (ppm)	1.69 $\pm$ 0.17	NA	
pH	8.74 $\pm$ 0.25	NA	
Conductivity (µS cm ⁻¹)	159.21 $\pm$ 17.99	NA	
NH ₄ (µg L ⁻¹)	8.85 $\pm$ 3.64	NA	
PO ₄ (µg L ⁻¹)	19.77 $\pm$ 4.97	17.12 $\pm$ 1.55	0.88
NO ₃ (µg L ⁻¹)	32.38 $\pm$ 21.09	11.69 $\pm$ 4.48	0.63
NO ₂ (µg L ⁻¹)	1.12 $\pm$ 0.36	0.41 $\pm$ 0.06	0.07
Depth to permafrost (cm)	35.6 $\pm$ 2.4	46.2 $\pm$ 2.2	<0.01

p values are from Mann–Whitney *U*-tests

evenness, and community composition in either year. Diatom diversity and evenness were also homogeneous in time, with no significant year effect on Shannon index score (2.50 ± 0.08 in Year 1, 2.46 ± 0.08 in Year 2, Mann–Whitney U -test $p = 0.79$) or evenness (0.76 ± 0.02 in Year 1, 0.73 ± 0.02 in Year 2, $p = 0.48$). On the other hand, community structure differed between the 2 years (npMANOVA, $p = 0.03$, $R^2 = 0.12$), with a substantial switch in dominant species identity (Fig. 2). In Year 1, *Luticola austroatlantica* was the most abundant diatom by a wide margin ($19.72 \pm 3.24\%$ of the community), followed by *L. macknightiae* ($= L. muticopsis$ f. *evoluta*) ($10.66 \pm 2.46\%$) and *L. mutica* ($10.53 \pm 1.71\%$). In Year 2, *L. macknightiae* almost doubled its relative abundance ($19.84 \pm 4.07\%$), becoming co-dominant with *L. austroatlantica* ($17.88 \pm 2.77\%$), while *L. mutica* dropped by almost half ($6.19 \pm 1.47\%$).

Invertebrate abundance

Total invertebrate abundance differed between years more in mats than in sediment (year $\times$ microhabitat interaction, $F_{1,24} = 4.33$, $p = 0.04$): in mats it was five times higher in Year 1, whereas in sediment it was slightly but non-significantly higher in Year 2 (Fig. 3a, b). As a result, while in Year 1 invertebrate abundance was more than one order of magnitude higher in mats than in sediment (paired Mann–Whitney U -test, $p < 0.001$), in Year 2, the difference between the microhabitats was non-significant ($p = 0.09$) and tended towards the opposite direction, that is, higher abundance in sediment. Patterns in mat invertebrate abundance expressed per area vs per dry weight of mat were similar (Online Resources 2), indicating that it was not an artefact of mat loss. Rotifers (represented by a single morphospecies) were

the most abundant group, and the large nematode *Eudorylaimus* sp. was the least abundant (Table 3 and Online Resources 2). Rotifers and tardigrades (the latter also a single morphospecies, *Acutuncus antarcticus*) followed the same patterns and dominated total abundance responses to microhabitat and years. By contrast, the two nematode taxa showed distinct patterns: in Year 2, *P. frigophilus* was equally abundant in mats and sediment, whereas *Eudorylaimus* sp. was more abundant in sediment (Table 3).

The difference in total invertebrate abundance between Year 1 and Year 2 was greatest upstream and decreased downstream in mats, whereas in sediments there was an opposite but weaker pattern (Fig. 3). These spatial patterns were followed by rotifers and the two nematode genera, but not by tardigrades. Normalizing invertebrate density by AFDM content in the mats did not change the results. There was no statistical support for a relationship between physico-chemical properties and total invertebrate abundance. *P. frigophilus* was the only taxon showing a relationship with physico-chemical properties, as in Year 1 it was more abundant at sites with lower DOC concentrations (Spearman's $r_s = -0.80$, $p = 0.02$).

Invertebrate community composition and diversity

Invertebrate Shannon diversity was low and did not differ between mats and sediment, but it differed significantly between years ($F_{1,24} = 8.24$, $p < 0.01$), being higher in Year 2 (1.04 ± 0.06 vs. 0.86 ± 0.06 in Year 1). Evenness was low and homogeneous, ranging from 0.30 to 0.86 in Year 1 and from 0.39 to 0.99 in Year 2, with no clear spatial or temporal differences. No statistical relationships were

Fig. 2 Relative abundances of the most common diatom species in the two sampling years. Abbreviation codes: Laustro = *Luticola austroatlantica*, Lmack = *L. macknightiae* ($= L. muticopsis$ f. *evoluta*), Lmutica = *L. mutica*, Hamph = *Hantzschia amphioxys*, Habun = *H. abundans*, Lreducta = *L. muticopsis* f. *reducta*, Lmuticop = *L. muticopsis*, Lperm = *L. muticopsis* var. *capitata*, Hhype = *H. hyperaustralis*, Ldolia = *L. dolia*

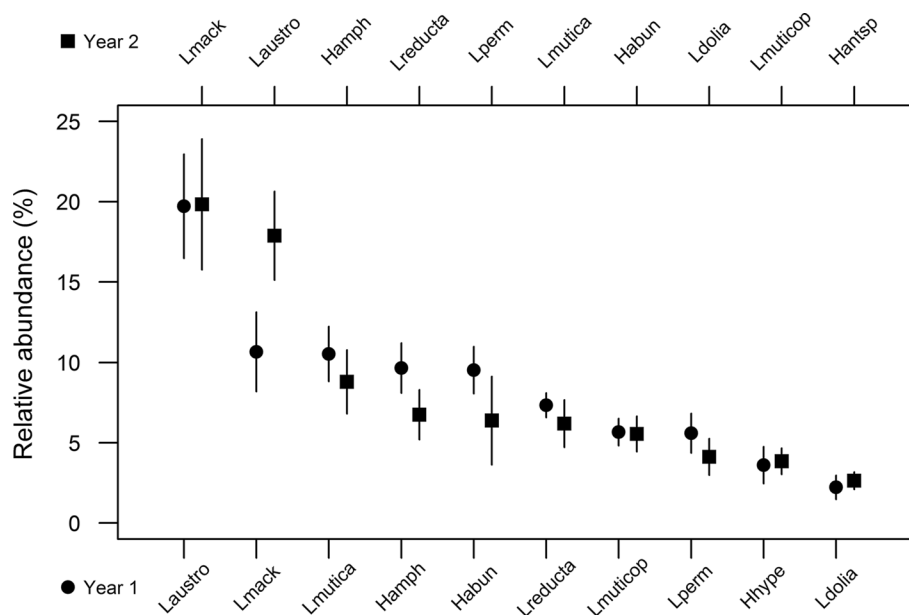


Fig. 3 Invertebrate density (individuals per g of substrate, mean $\pm$ SE) in **a** cyanobacterial mats and **b** underlying sediment, and **c** the difference between invertebrate density in Year 1 and Year 2 along the stream (left = upstream, right = downstream). *p* values in **(a)** and **(b)** are based on *F*-tests of mixed-effect models. Curvilinear equations in **(c)** were fit by log-transforming distance from upper stream

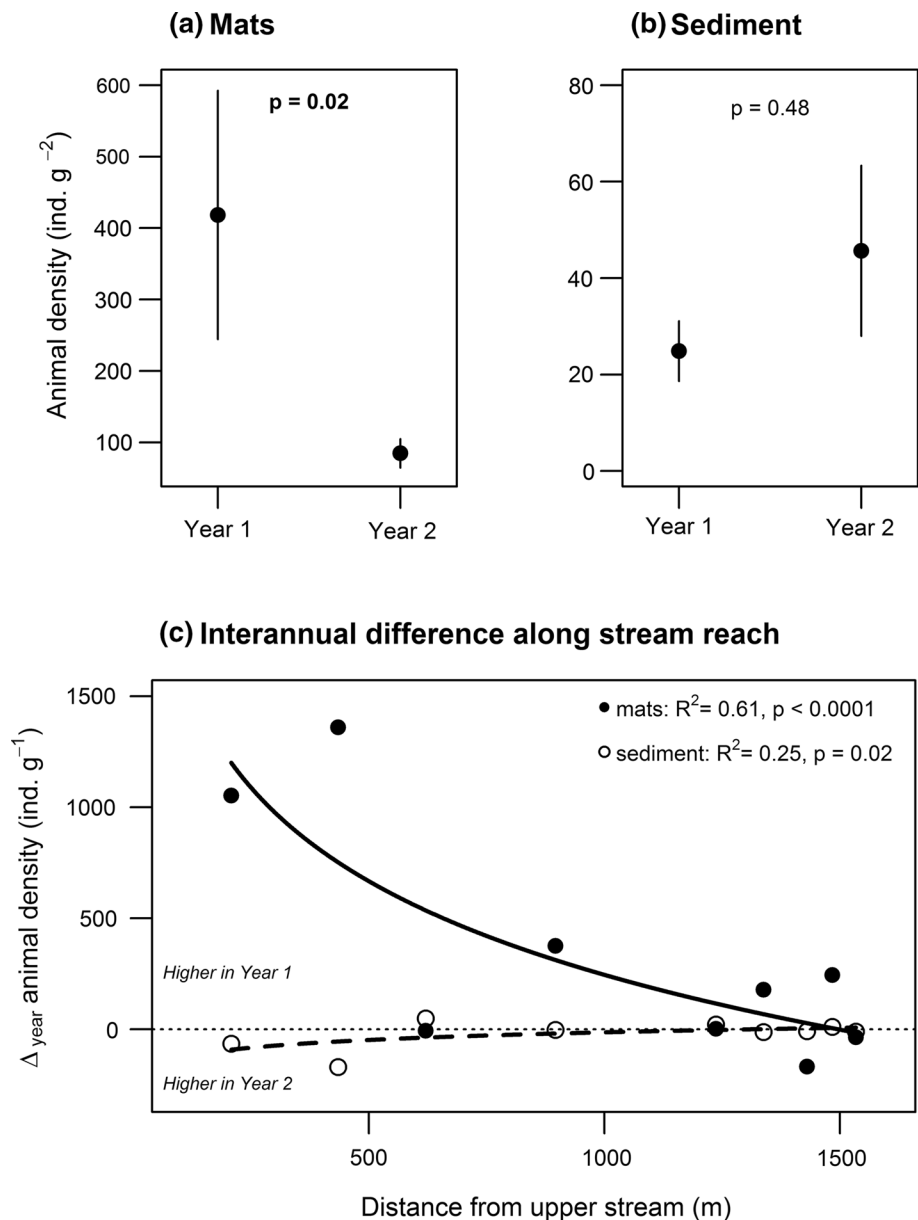


Table 3 Invertebrate density (individuals per g of substrate, mean $\pm$ SE) in cyanobacterial mats (M) and the underlying sediment (S) of the reactivated stream in Taylor valley, Antarctica ($n=9$ per microhabitat per year)

Taxon	Microhabitat	Year 1	Year 2
Rotifers	M	307.51 $\pm$ 157.18	39.92 $\pm$ 14.73
	S	16.26 $\pm$ 5.64	13.43 $\pm$ 4.32
Tardigrades	M	76.59 $\pm$ 19.98	22.30 $\pm$ 5.64
	S	2.64 $\pm$ 0.47	16.99 $\pm$ 11.10
<i>P. frigophilus</i> .	M	24.20 $\pm$ 10.48	21.41 $\pm$ 9.35
	S	2.11 $\pm$ 0.62	9.90 $\pm$ 4.33
<i>Eudorylaimus</i> sp.	M	10.04 $\pm$ 4.61	2.07 $\pm$ 0.85
	S	3.94 $\pm$ 2.11	5.34 $\pm$ 1.52
Total	M	418.34 $\pm$ 137.90	84.71 $\pm$ 20.15
	S	24.85 $\pm$ 6.22	45.66 $\pm$ 17.68

found between invertebrate Shannon index score or evenness and physico-chemical properties.

Invertebrate community composition differed between mats and sediments more in Year 1 (npMANOVA: $p < 0.001$, $R^2 = 0.31$) than in Year 2 ($p = 0.02$, $R^2 = 0.13$). When both years were analysed together, npMANOVA separated the samples by microhabitat ($p < 0.01$, $R^2 = 0.18$) but not by year or its interaction with microhabitat. Weak variation in community composition was explained by location along the stream in both years ($p = 0.062$, $R^2 = 0.09$ in Year 1; $p = 0.07$, $R^2 = 0.28$ in Year 2).

Relationships between invertebrates, microbial mat biomass, and diatoms

Across both years, AFDM was negatively correlated with total invertebrate abundance (Spearman's $r_s = -0.50$, $p = 0.04$) and in particular with nematodes (Spearman's $r_s = -0.52$, $p = 0.03$); likewise, chlorophyll *a* concentration negatively correlated with nematodes (Spearman's $r_s = -0.52$, $p = 0.03$). When separating the two sampling years, however, these negative relationships were significant only in the first. In Year 1, chlorophyll *a* concentration correlated negatively with total nematode abundance (Spearman's $r_s = -0.78$, $p = 0.02$), and also individually with both *P. frigophilus* (Spearman's $r_s = -0.76$, $p = 0.02$) and *Eudorylaimus* sp. (Spearman's $r_s = -0.73$, $p = 0.03$). In Year 1, AFDM also correlated negatively with *P. frigophilus* (Spearman's $r_s = -0.80$, $p = 0.01$) and, marginally, with *Eudorylaimus* sp. (Spearman's $r_s = -0.71$, $p = 0.06$). Ratio of chlorophyll *a* to AFDM in Year 1 was significantly related to lower *Eudorylaimus* sp. abundance (Spearman's $r_s = -0.71$, $p = 0.03$). These species-specific correlations were also negative but not significant in Year 2. Invertebrate abundance, whether in total or for single groups, was not statistically related to community dissimilarity, diversity, and evenness of diatoms. The main correlations are shown in Online Resources 2.

Discussion

Flow as the overriding driver of MDV microbial mat communities?

We found that invertebrates in microbial mats along an Antarctic stream were much more abundant in a growing season characterized by low air temperatures and weak flow (Year 1, i.e. summer 2007–2008). Rotifers were overall almost 10 times more abundant, and tardigrades and *Eudorylaimus* sp. were, respectively, 3.5 and 5 times more abundant, in the low-flow year (Fig. 3, Table 3). By contrast, AFDM and chlorophyll *a* content, which indicate total and phototrophic biomass respectively, were higher in the following growing season (Year 2, i.e. summer 2008–2009), which was warmer and characterized by peak flows above 100 L s^{-1} , the estimated threshold for significant scouring of the mats in MDV streams (Cullis et al. 2014). Although our study examined only 2 years, evidence from previous studies in MDV streams strongly suggests that these biological patterns can be at least partly attributed to the differences in streamflow. At short time scales, MDV mats are controlled by growth during periods of flow and biomass loss during the daily pulse of water that occurs as a result of changes in sun angle and high flow periods (Cullis et al. 2014). At

longer time scales, microbial and diatom responses to inter-annual variation in water availability and streamflow are well studied in the MDVs (McKnight et al. 2007; Stanish et al. 2012; Cullis et al. 2014), and it has been shown that scouring under high flow conditions decrease mat biomass (Kohler et al. 2015b). So far, however, the responses of invertebrates in MDV mats to streamflow variation had not been studied.

Invertebrate abundance in Year 1 was similar to that measured in streams in a nearby site during 2006–2007 (Simmons et al. 2009), which was also a low-flow season (Online Resources 1). In Year 2, invertebrate abundance in the mats dropped considerably, and we suggest disturbance under high flow as the likely cause. A portion of the invertebrate community may have flushed from the epilithon matrix under the higher flow conditions. Experimental tracer studies in a nearby MDV stream have shown that water in the microbial mats continuously exchanges with water in the overlying channel (Gooseff et al. 2004) and the movement of water through the mats may be greater under higher flows. Further, higher flows and entrainment of fine sediment could cause a decrease in the cohesive nature of the mat matrix itself, which may have contributed to the decline in invertebrates. In fact, the difference in mat invertebrate abundance between Year 1 and Year 2 was much stronger in the upstream reaches, where the relative increase in flow velocities might have been greater given the steeper gradient in the lower channel; in the downstream reaches the gap in mat invertebrate abundance between Year 1 and 2 was reduced or overturned (Fig. 3c). By contrast, in the sediment, which was sheltered from the physical disturbance of the peak flows, the difference in invertebrate abundance between Year 1 and Year 2 was much reduced, and tended to increase along the stream reach. Overall, these results suggest that mat invertebrates were negatively impacted by high flow disturbance, and that the sediment underneath may act as a refuge for the invertebrates.

In contrast to the invertebrates, mat biomass was greater in Year 2, as indicated by higher AFDM and chlorophyll *a* content. Low temperatures and occasional dehydration in Year 1 were probably more limiting to algal biomass than the physical disturbance of scouring flows in Year 2. The shifts in diatom species abundance we observed from Year 1 to Year 2, on the other hand, are consistent with previous studies in the MDV streams (Stanish et al. 2011), with some species benefiting from the high flow velocity disturbance at the expense of others (e.g. *L. macknightiae* overcame *L. austroatlantica* as the most common species). Multivariate analysis of biomass and physico-chemical properties showed that the spatial variation along the stream differed between years (location $\times$ year interaction), as nitrate and phosphate were by far highest at the downstream sites in the low-flow year. We found no clear relationships between physico-chemical properties and microbial mat biological

properties in each year, despite a threefold variation in depth to permafrost along the stream reach and more than twofold variation in salinity. This may be partly because of lagged effects of previous years' conditions on these perennial mats.

Top-down effects of invertebrates in MDV streams?

We found negative correlations of mat total and phototrophic biomass with nematode abundance during the low-flow Year 1, when AFDM and chlorophyll *a* negatively correlated to nematode abundance, in total and for both *P. frigophilus* and *Eudorylaimus* sp. No significant relationships were found in Year 2, in which AFDM and chlorophyll *a* were higher than in the previous year while invertebrate abundance was much lower. It is possible that mats with more algal biomass were worse habitats for the nematodes, e.g. due to reduced pore space for movement. Another explanation is that those correlations are signatures of top-down grazing effects of the nematodes on microbial mat biomass. This raises the possibility that invertebrates exert detectable top-down effects on primary production in the MDVs, an ecosystem in which biological communities are thought to be structured predominantly by abiotic factors (Convey et al. 2014). In MDV soils, biotic interactions are weak (Hogg et al. 2006), but stronger interactions are conceivable in streams, where productivity and amounts of contemporary organic matter originated by photosynthesis are much greater. Studies on microbial biofilms in non-polar epibenthic food webs showed that grazing by rotifers and nematodes on bacteria and microalgae may be significant (Arndt 1993; Borchardt and Bott 1995; Epstein 1997), and that microinvertebrates regulate microbial communities and nutrient dynamics by feeding, excretion, and bioturbation (Derlon et al. 2013; Majdi and Traunspurger 2015). Knowledge on the feeding ecology of MDV stream invertebrates in situ is limited, but various sources suggest that the taxa in our study have the potential to feed on the lower trophic levels in the microbial mats. Rotifers, tardigrades and *P. frigophilus* in the study region are bacterial feeders (Freckman and Virginia 1997; Adams et al. 2014), and rotifers also feed on cyanobacteria (Gaudes et al. 2006; Mialet et al. 2013), tardigrades feed on both cyanobacteria and green microalgae (Kagoshima et al. 2013; Tsujimoto et al. 2015), and the large omnivore *Eudorylaimus* sp. from moist soils was shown to consume microalgae (Wall 2007). Recently, Shaw et al. (2018) demonstrated that *Plectus*, rotifers, and tardigrades in wet soils at the margin of MDV streams are indeed mat grazers. Moreover, observations on temperate biofilms showed that rotifers and bacterial-feeding nematodes may feed on diatoms (Neury-Ormanni et al. 2016) and that bacterial-feeding nematodes may selectively graze on microbes associated with cyanobacterial

filaments (Gaudes et al. 2006; Majdi and Traunspurger 2015). Considering these findings, our results on the correlations between mat biomass and nematodes, although not conclusive evidence by themselves, raise the question of whether invertebrate grazers would control algal and biofilm biomass in MDV streams. Such trophic interactions have not been documented in the MDVs, or in other high latitude ecosystems, but to our knowledge no study has tested whether they may occur.

Concluding remarks

Because our study was observational, cause–effect relationships cannot be conclusively inferred, but integrating our findings with previous studies in MDV streams we offer the following predictive hypotheses: (1) scouring under high flow conditions leads to strong declines in mat invertebrates; (2) under such disturbance, sediment under the mats is a refuge for the invertebrates. These hypotheses are also relevant beyond the MDVs, as well-developed cyanobacterial mats also occur in the Arctic (Vincent and Quesada 2012; Tytgat et al. 2014), and less conspicuous but ecologically similar biofilms with abundant micro-meiofauna are a common feature of many aquatic–terrestrial interfaces (Grimm and Petrone 1997; Paerl et al. 2000). Testing our hypotheses could therefore improve our understanding of microbial biofilm ecology in a wide range of environments. An additional hypothesis suggested by our results is that, in the absence of high flow disturbance, microbial mat productivity could be top-down limited by invertebrate grazers, even when the latter do not include macroscopic animals. Such a hypothesis challenges a knowledge gap about the importance of biotic interactions in the MDVs, which is currently thought to be limited. Should it be validated in future studies, a follow-up question would be whether limitations of the abundance and activity of microscopic invertebrate grazers under conditions of high flow contribute to the accumulation of microbial biomass and subsequent nutrient immobilization in MDV streams.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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