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Hydrologic processes influence diatom community composition in Dry Valley streams

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Abstract. Our paper describes the ecological controls on algal-mat diatom communities in the dynamic stream ecosystems of the McMurdo Dry Valleys in Antarctica. Dry Valley diatom communities are relatively diverse, and nearly ½ of the taxa found in these mats are considered endemic. Diatom community composition was examined in 5 streams in Taylor Valley during a 15-y cooling period that included a discrete flood event. Two hydrologic variables, total annual discharge and historical variation in discharge, gave the most parsimonious model of among-stream and interannual variation in diatom communities. Algal-mat biomass and chlorophyll *a* concentrations decreased after the flood, which occurred during the 2001/2002 summer season. Most algal-mat diatom communities recovered quickly after the flood. However, Green Creek, a relatively high-flow stream with low historical variation in discharge, appears to have experienced a persistent diatom community shift toward increased relative abundance of small, generalist species. Diatom relative biovolume, a proxy for the size of diatoms within a sample, was negatively correlated with stream flow, such that higher-discharge streams contained greater relative abundances of smaller diatoms than lower-flow streams. Therefore, diatom size may play a role in determining the distribution of a species in these streams and may be useful for monitoring environmental changes. Our study demonstrates the importance of understanding factors affecting ecosystem resilience, especially in polar regions, which are experiencing rapid climate changes.

Key words: diatoms, streams, Antarctica, hydrology, community ecology, ecological indicators.

Hydrologic disturbances and flow regime lay the foundation for stream ecosystem functioning and community development (Peterson 1996, Biggs and Smith 2002). The importance of flow variability is evident in intermittent rivers, and its role in maintaining biodiversity and ecosystem health is increasingly recognized in regulated systems across the globe (Poff et al. 2007). Low-flow disturbances occur frequently in hot and cold desert streams and can desiccate stream algal mats. Few studies have examined the effects of these disturbances on diatom communities in situ. In one study, low-flow disturbance events altered long-term algal assemblages such that the mature community was better adapted to both high- and low-flow extremes (Ledger et al. 2008). Furthermore, certain desert diatoms are physiologically capable of surviving dry periods (Hostetter and Hoshaw 1970), and other diatoms may be protected by existing within desiccation-resistant biofilms or microbial mats produced by other members of the microbial community (Peterson 1987, Davey 1989).

In polar environments, diatoms in algal mats appear to be influenced by hydrologic regime. For example, in the high Arctic, Antoniades et al. (2009) found that differences in diatom communities across 42 streams could not be explained by water chemistry or geography alone and postulated that a dynamic, meltwater-driven flow regime may influence diatom communities. Resilience was shown in a Canadian Arctic stream, where diatom communities quickly returned to predisturbance conditions after a high-flow event (Stewart et al. 2005).

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The glacial meltwater streams in the McMurdo Dry Valleys of Antarctica provide an ideal environment in which to study diatom community changes in the context of variable flow. Significant hydrologic fluctuations occur throughout a season, similar to intermittent desert streams (Stanley et al. 1997, Conovitz et al. 1998). The dynamic hydrologic regime is characterized by periods of desiccation and episodic high flows, which are pronounced in longer streams with higher-elevation source glaciers (Conovitz et al. 1998). In addition, the benthic algal mats are trophically simple ecosystems (Virginia and Wall 1999, Cary et al. 2010) situated in a pristine environment, thereby allowing us to better examine how physical processes drive ecosystem dynamics. Unlike algal mats found in temperate or tropical streams, Dry Valley mats are perennial, surviving the long winter months in a freeze-dried state and rapidly resuming metabolism at first flows, even after years of dormancy (Vincent and Howard-Williams 1986, McKnight et al. 2007). This desiccation tolerance is facilitated by cyanobacteria, which dominate stream algal mats and provide a stable matrix for the relatively diverse diatom flora. Last, algal-mat diatom communities consist of numerous putative endemic species that appear to be adapted to the dynamic hydrologic regime (Esposito et al. 2006).

Antarctic Dry Valley ecosystems are driven by the availability of liquid water, which can vary significantly as a result of both long- and short-term and physical forcings. The McMurdo Dry Valleys have experienced a cooling trend from 1966 to the present—particularly during the biologically active summer seasons (1966–2000 [Doran et al. 2002], 2001–present [http://www.mcmlter.org]). From 1966–2000, discharge from 8 streams into Lake Fryxell decreased at a rate of 1.8×10^5 m^3/y (Doran et al. 2002). Ecosystems responded to decreased summer temperatures with reduced lake primary productivity and soil nematode populations (Doran et al. 2002). The cooling period also increased relative abundances of endemic diatoms in streams (Esposito et al. 2006), but the species or communities responsible for this relationship have not been investigated. Conversely, a discrete warming event—referred to as the flood year—occurred within the cooling period in 2001/2002, which rapidly increased stream flows, lake levels, soil moisture content, and nutrient export to lakes (Foreman et al. 2004, Barrett et al. 2008). The resulting increase in water availability altered soil nematode populations (Barrett et al. 2008) and temporarily increased lake primary productivity (Foreman et al. 2004). However, the effects of the flood year on diatom communities have not been addressed.

The goal of our study was to characterize the environmental controls on diatom community composition in Dry Valley streams temporally and across streams. Diatom communities were determined from algal-mat cores collected as part of the McMurdo Dry Valleys Long-Term Ecological Research (MCMLTER) program. Interannual variation in diatom communities was assessed across 5 streams in Taylor Valley from 1993–2008 and was correlated to a variety of environmental variables. Based on the results of Esposito et al. (2006), we expected that hydrology would be an important regulator of diatom community composition.

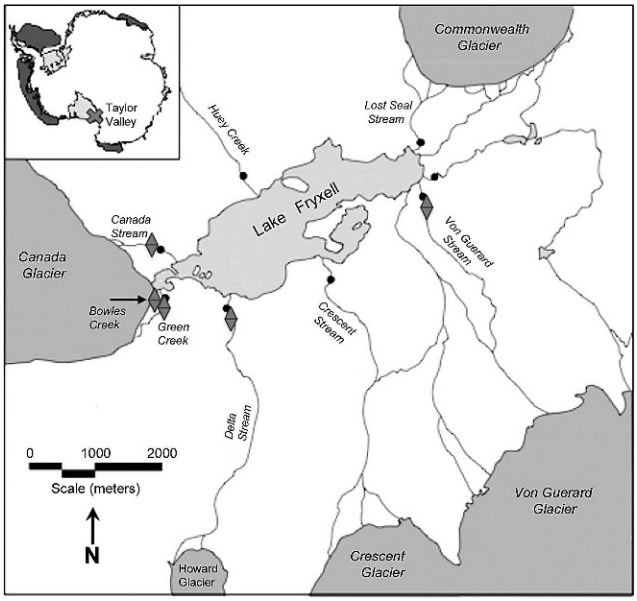


FIG. 1. Overview of Lake Fryxell basin, Taylor Valley, Antarctica. Locations of algal-mat transects analyzed in our study are marked with diamonds. Circles indicate locations of stream discharge gauges. Bowles Creek, marked with an arrow, lies west of Green Creek and does not have a stream gauge. Map adapted from Gooseff et al. 2003.

Methods

Study site

The Dry Valleys are among the coldest and driest habitats on the planet and comprise the largest ice-free region on the Antarctic continent. This topographically diverse landscape contains a series of valleys punctuated by mountain ranges running from the Ross Sea to the Polar Plateau (Fig. 1).

Dry Valley stream beds are dry for most of the year and become active for 6 to 12 wk during the austral summer. During this period of 24-h sunlight, incoming shortwave radiation generates glacial meltwater, which drains via ephemeral streams into closed-basin lakes on the valley floors. The streams are important

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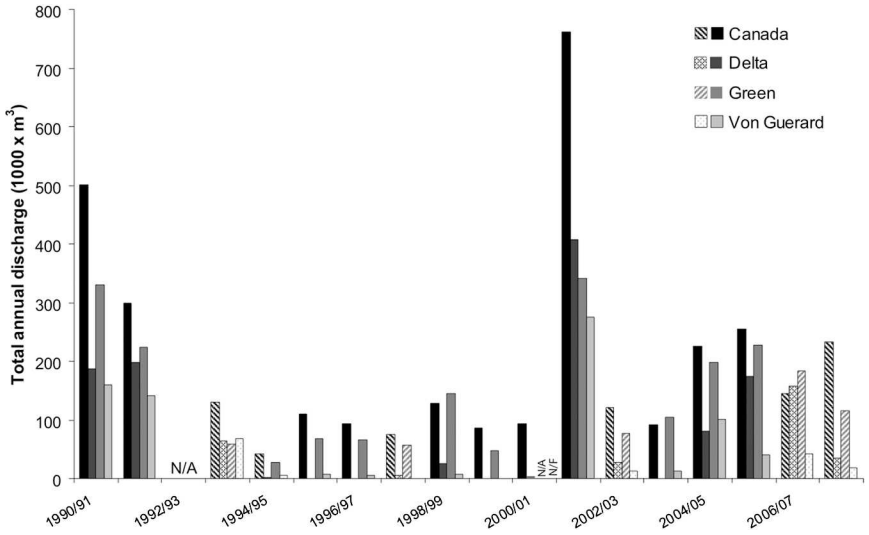


FIG. 2. Total annual discharge records for Canada Stream, Delta Stream, Green Creek, and Von Guerard Stream from 1990 to 2008. Seasons in which diatom samples were analyzed are indicated with hatches. Solid bars indicate seasons in which diatom data were not analyzed. N/A = no discharge data available, N/F = no flow observed.

sites for nutrient cycling (Gooseff et al. 2004, McKnight et al. 2004), support a relatively diverse suite of organisms and biological activities, and influence the water budget of the Dry Valley ecosystem. Streams retain meltwater through hyporheic storage and lose water via evaporation and biological metabolism (Conovitz 2000, Gooseff et al. 2003, Cozzetto et al. 2006). Weathering reactions in the hyporheic zone are the primary sources of ions, such as Si and K, to the water column (Lyons et al. 1998, Gooseff et al. 2002). Stream water temperature is highly variable, ranging from 0.1 to 15°C, and stream flow can vary 5 to 10× in a 24-h period depending on the sun angle (Conovitz et al. 1998, Cozzetto et al. 2006). Stream flow has been monitored at gauging stations on streams in Taylor Valley since the 1990/1991 summer season. These records demonstrate the high variability in annual stream flow across streams and seasons. For instance, the total annual volume of water flowing in Canada Stream is 2 to 17× higher than that flowing in Von Guerard Stream (Fig. 2). Also, infrequent flood years, such as occurred during the 2001/2002 season, can increase total annual discharge as much as 15× above the average for the recorded period.

In Antarctic algal mats, cyanobacteria are numerically dominant and have been studied with regard to taxonomy (Howard-Williams et al. 1986, Vincent et al. 1993, Alger et al. 1997, Taton et al. 2003, Comte et al. 2007, Komárek et al. 2008), primary production (Howard-Williams and Vincent 1989, McKnight and Tate 1997), and responses to desiccation (Davey 1989). In fine-scale examination of cyanobacterial mats, distinct layers were found that may prevent UV damage and desiccation and retain nutrients (Davey and Clarke 1992, Vincent et al. 1993). Spatial variability in stream algal-mat microbial communities is evident based on mat color, which changes depending on dominant cyanobacterium present (Howard-Williams et al. 1986). Within the main channel, algal mats are dominated by Oscillatoriales and appear orange or grey/brown. Along the stream margins, algal mats appear black because of high abundances of members of the order Nostocales. Additional mat types exist within the main channel on the under side of rocks or in the main channel as thick, rubbery mats, and combinations of mat types can be found in regions of variable flow.

The diatom flora of Dry Valley streams has been well characterized morphologically (Kellogg et al. 1980, Spaulding et al. 1997, Sabbe et al. 2003, Esposito et al. 2008). A complete list of Antarctic stream diatom taxa and currently known distributions can be found in Esposito et al. (2008). Of 41 stream diatom species, 17 have a current distribution that does not extend beyond the Antarctic continent (Esposito et al. 2008). These endemic species are distributed throughout Dry Valley streams at high relative abundances.

Algal mat samples were collected from 5 glacial meltwater streams—Von Guerard Stream, Delta Stream, Green Creek, Bowles Creek, and Canada Stream (Fig. 1). Algal mat transects located on each stream were sampled every 2–3 y as part of the MCMLTER program (Alger et al. 1997). The transects

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TABLE 1. Physical characteristics of streams examined in this study. Mean total annual discharge (TotQ) represents the average total daily discharge measured during a summer season from 1990/1991 to 2007/2008, excluding 1992/1993 and 2000/2001. Qvarhist = maximum annual discharge/minimum annual discharge for the 1990–2008 time period.

Stream	Mean TotQ (m^3)	Qvarhist	Mean season length (d)	Stream length (km)	Algal coverage[a]
Bowles	2.62×10^{4}[b]	12.5[b]	57[b]	0.9	High
Canada	2.06×10^{5}	18.2	71	1.5	High
Delta	1.05×10^{5}	531.3	55	11.2	Low
Green	1.42×10^{5}	12.5	57	1.2	High
Von Guerard	5.97×10^{4}	383.6	44	4.9	Low

[a] From Alger et al. 1997
[b] Estimated

were chosen to represent similar habitats and are near the discharge gauging stations.

Von Guerard Stream is the 2nd-longest (4.9 km) stream within the Fryxell Basin. The source glacier is at a high elevation in the Kukri Hills, resulting in a later flow season and higher discharge variability within the season and interannually (Table 1). The transect site is in a braided region of the stream channel where the stream has a low gradient and the rocks are arranged in a stable stone pavement (McKnight et al. 1999) that becomes less stable toward the stream margins. Algal mats have a patchy distribution and are predominantly black and orange.

Delta Stream is fed from the Howard Glacier and is the longest (11.2 km) stream in the Fryxell Basin. Flow begins later in the season but persists longer into February because of greater storage of water in the extensive hyporheic zone and in upland ponds. This stream has the highest historical variation in discharge of the 5 streams examined in our study (Table 1). At the transect site, the channel widens and seeps develop that connect with the main channel along the western edge of the stream bed. Some larger cobbles are present at a riffle, whereas the rest of the stream bed consists of coarse sand and has a shallow gradient. Orange mats occur in a narrow zone within the thalweg, whereas filamentous mats dominated by green algae and black mats occur in patches throughout.

Green and Bowles Creeks are on the southwestern side of Lake Fryxell and are fed by meltwater ponds at the base of Canada Glacier. They are the shortest streams with lengths of 1.2 and 0.9 km, respectively. Both creeks have shallow gradients and well defined channels consisting of a stable stone pavement, but Green Creek has higher discharge and a much wider stream channel (Alger et al. 1997). Orange and black algal mats are abundant at each transect. Discharge is not actively monitored on Bowles Creek, but discharge in Bowles Creek is correlated with discharge in Green Creek (Alger et al. 1997).

Canada Stream is ~1.5 km long from its source on the tongue of Canada Glacier. It is one of the first streams in the Dry Valleys to begin flowing each summer and is one of the major sources of inflow to Lake Fryxell. The stream bed contains mostly cobbles and rocks that are arranged in a stable pavement. Along the stream margins, the stream bed becomes less stable with smaller particles. Orange, black, and green algal mats are abundant at this transect. Upstream of the transect, meltwater flows through a large pond at the base of the glacier.

Hydrologic and chemical data collection

Biological and environmental data used in our study were collected as part of the MCMLTER (available from: www.mcmlter.org). Discharge data were collected continuously by pressure transducers installed at gauge sites on Von Guerard Stream, Canada Stream, Green Creek, and Delta Stream (Fig. 1) and logged at 15-min intervals throughout the austral summer. Discharge at Bowles Creek was estimated based on the correlation between 3 manual discharge measurements collected from Green Creek and Bowles Creek during the 2009/2010 flow season. The linear equation is: $y = 0.1847x - 0.0229$ ($r^2 = 0.93$).

Stream water was collected during weekly hydrologic site visits conducted throughout the flow season. Raw water samples were collected in triple-rinsed 250-mL Nalgene® bottles, and water for dissolved organic C (DOC) analysis was collected in 125-mL amber precombusted glass 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. DOC was filtered and acidified using concentrated HCl and stored at 4°C for later analysis. All chemistry analyses were performed at the Crary Laboratory at McMurdo Station. The mean values of all water-chemistry samples collected during a season were used in our study.

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Algal-mat collection and preparation

Algal-mat samples analyzed in our study were collected early to mid-January from similar habitat and mat types to control for variation that might be attributable to these characteristics. Algal-mat samples were orange and were collected from the stable stone pavement areas of the main channel in each stream. Mats were collected using a brass cork borer (1.7 cm diameter) and placed in Whirl-Pak® bags containing 10 to 15 mL stream water. Samples were preserved in 10% formalin and shipped to the University of Colorado at room temperature. Replicate samples were limited for some streams, so an equal representation of samples from each stream and season was maintained by analyzing 1 sample from each stream during each season for which data were available. Representative mat samples were chosen at random or to maximize the availability of complementary biomass data. Samples were analyzed during the following seasons: 1993/1994 (all 5 streams), 1994/1995 (Canada Stream and Green Creek), 1997/1998 (Canada Stream, Delta Stream, Green Creek, Von Guerard Stream), 2002/2003 (all 5 streams), 2006/2007 (all 5 streams), and 2007/2008 (Canada Stream, Delta Stream, Green Creek, Von Guerard Stream). More samples were available from Green Creek and Canada Stream than from other streams. Therefore, replicate algal mat samples collected from these 2 streams were used in a separate analysis to determine the effect of interannual variation on diatom community composition. Replicates were collected at the same time along the transect. For this analysis, 1 to 4 mat samples were analyzed for each time point to the extent that samples were available.

Chlorophyll *a* (Chl-*a*) and ash-free dry mass (AFDM) analyses were conducted on algal-mat samples that were collected in conjunction with diatom sampling events or as ancillary data for other stream studies. Whether or not diatom samples were collected, all algal-mat samples for biomass analyses were collected in January and at the same transect sites with similar coring methods as described above. Samples were dewatered on precombusted Whatman GF/C® filters, wrapped in foil, and stored at −20°C. Prior to the year 2000, Chl-*a* was extracted in buffered acetone and analyzed spectrophotometrically with the trichromatic method. After 2000, Chl-*a* was extracted in buffered acetone and analyzed using a Turner Designs 10-AU field fluorometer (Turner Designs, Sunnyvale, California). The 2 methods produce comparable Chl-*a* results (Lorenzen and Jeffrey 1980). For AFDM analysis, samples were dried at 100°C for 24 h, weighed, burned at 450°C for 4 h and reweighed, and then rewetted and dried to determine mass loss caused by hydration of sediments. Both Chl-*a* and AFDM analyses were done at Crary Laboratory in McMurdo Station.

Algal-mat samples used for community analysis were digested using heat and H_2O_2 and rinsed several times with distilled water. Examination of oxidized material limits the ability to distinguish live from dead cells, but this method was necessary to make accurate species-level identifications. Based on the presence of chloroplasts in intact cells, 50 to 77% of the diatoms were alive at the time of sampling. A subset of the digested material was dried onto cover slips and permanently mounted on glass microscope slides with the mounting medium Zrax (W. P. Dailey, University of Pennsylvania). Relative abundances of diatom species were determined using an Olympus Vanox light microscope (Japan) at 1250× magnification, with ≥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), and the Antarctic Freshwater Diatoms database (http://huey.colorado.edu/diatoms). The taxonomic identity of *Psammothidium chlidanos*, as defined by Spaulding et al. (1997) and Esposito et al. (2008), is under revision. It is referred to here as *Psammothidium* sp. #1 and may constitute a new species. In comparison to *Psammothidium chlidanos*, our specimens have coarser striae (25–28/10 μm vs 27–33/10 μm) and a more elongated central area in the pseudoraphe valve. Compared with its Antarctic relative, *Psammothidium metakryophilum*, our specimens are larger (length 14.3–16.2 μm × width 5.0–5.8 μm vs 9–12 μm × 4.3–5.2 μm).

Data analysis

Diatom community composition was analyzed using a variety of multivariate methods. Statistical analyses were done with Primer-E (Clarke and Gorley 2006) and the R software package (R Development Core Team, Vienna, Austria). For analyses that required a distance matrix of diatom communities, rare species occurring at <0.4% relative abundance (<~1 valve in a given sample) were removed, and a distance matrix of relative abundance counts was calculated based on Bray–Curtis dissimilarity. Diatom community diversity (SW) was calculated with the Shannon–Wiener index

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

where p_i is the relative abundance of species i and S is the number of species. Evenness was calculated as the ratio of H' to H'_{max}, which equals ln$S$.

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TABLE 2. Description of hydrologic variables.

Environmental variable	Description
AvgMinQ	Mean daily minimum discharge for the entire flow season
AvgMaxQ	Mean daily maximum discharge for the entire flow season
AvgQ	Mean daily discharge for the entire flow season
TotQ	Total discharge for the entire flow season
MaxOverAvg	AvgMaxQ – AvgQ
MinBelowAvg	AvgQ – AvgMinQ
SeasonLength	Number of days from the start of flow until the end of flow
FlowDays	Number of days during a flow season when flow was >0
Qvarhist	Maximum annual discharge/minimum annual discharge for the 1990–2008 time period
Qvarseason	TotalQ/AvgQ during the 1990–2008 time period

Nonmetric multidimensional scaling (NMDS) is an ordination method that reduces the complexity of community data into fewer dimensions. This method can use any distance matrix, making it useful for community data. The nonmetric ordination method replaces intersample distances with their ranks, which makes the method less sensitive to nonlinear relationships and discontinuous distributions. The method is iterative and repeats the ordination calculations at random starting points. Species are plotted at the center of their distribution across samples. NMDS was done on a Bray–Curtis dissimilarity matrix of diatom community data using the vegan package in R. A 3-dimensional model produced a goodness-of-fit value of 6.4% using Kruskal's stress formula. A Shepard plot of calculated vs raw dissimilarities showed strong nonmetric ($r^2 = 0.996$) and linear ($r^2 = 0.974$) fits.

Principal Components Analysis (PCA) was used to examine variation in environmental variables across streams. A Euclidean distance matrix of all environmental data was calculated using either log(x)- or $\sqrt{}$(x)-transformed and scaled data.

A metric for determining the relative size of diatoms within a mat community (diatom relative biovolume) was calculated based on the equation

$$BV = \sum_i x_i b_i$$

where x is the relative abundance of species i and b is the biovolume of species i. This metric differs from the standard sample biovolume calculation in that it represents only the biovolumes of the diatom species, which constitute a relatively minor proportion of the biomass of Dry Valley stream algal mats. Diatom biovolumes were calculated based on the geometric shapes for diatom genera outlined in Hillebrand et al. (1999). Mean lengths and widths were taken from the Dry Valley diatoms database (http://huey.colorado.edu/diatoms). Determining frustule depth is technically challenging, so all species were assumed to have the same average cell depth of 2 μm. This assumption may have led to underestimation of the sizes of larger species.

Hierarchical cluster analyses were done on diatom community data using Bray–Curtis distance matrices. The average linkage method was chosen because it produced a classification tree with the highest cophenetic correlation coefficient (which describes the similarity of the modeled distances to the original pairwise distances).

Sixteen physical and chemical variables were considered to develop an explanatory model for diatom community composition. The physical variables and their definitions are listed in Table 2. Historical variation in discharge (Qvarhist) represents the maximum factor of interannual variation in total annual discharge (TotQ) for a stream by dividing TotQ of the highest flow season on record by the TotQ of the lowest flow season on record to give a single value for each stream. The chemical variables considered were NO_3^-, NO_2^-, NH_4^+, soluble reactive P (SRP), DOC, and Si. The correlations between environmental variables and diatom community composition were determined using BEST analysis (PRIMER-E; Clarke 1993). This method maximizes the rank correlation between 2 distance matrices using Mantel-like tests, in which significance is tested via permutation (Mantel 1967). For environmental data, a Euclidian distance matrix was calculated on log(x)-transformed, normalized data.

Results

Stream-wide variation in environmental conditions and diatom communities

PCA of the environmental variables separated Von Guerard and Delta Streams from Green Creek, Bowles Creek, and Canada Stream (Fig. 3). PCA axis 1 was most strongly related to differences in hydrologic variables, whereas axis 2 was driven by differences in nutrient concentrations, flow variability, and flow frequency (Fig. 3). In general, Von Guerard Stream

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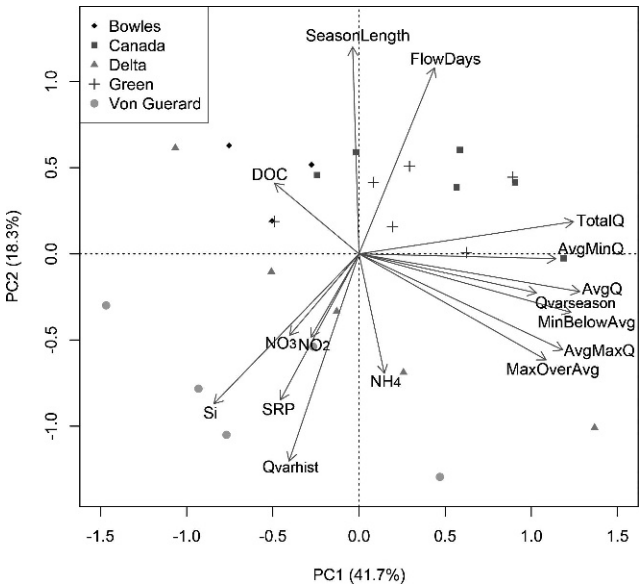


FIG. 3. Principal components analysis (PCA) of all environmental variables considered in our study. See Table 2 for description of variables and abbreviations.

and Delta Stream had higher nutrient concentrations and higher interannual variability in stream flow than Green Creek, Bowles Creek, and Canada Stream (Fig. 3, Table 1). Conversely, the 3 latter streams have longer growing seasons and, for Green Creek and Canada Stream, total annual discharge is higher (Table 1). Numerous chemical and physical variables were correlated. Qvarhist varied significantly with stream length ($R^2 = 0.90$, $p < 0.005$) and with ion concentrations, such as Na^+ ($R^2 = 0.91$, $p < 0.05$; Table 3). In contrast, SRP and other nutrients were not correlated to discharge variables (Table 3).

Algal-mat diatom species were ubiquitous across streams, and most species were present in most streams (Fig. 4). However, their relative abundances varied greatly among streams. *Hantzschia* species occurred in higher relative abundances in Bowles Creek, Delta Stream, and Von Guerard Stream. Species of the genus *Diadesmis* occurred more abundantly in Canada Stream throughout the study period and in Green Creek after the 2001/2002 flood year. *Luticola* species were in highest relative abundances in Delta Stream and Von Guerard Stream, but also dominated Green Creek before the flood.

To develop a model that best explained the observed diatom community results, combinations of environmental variables were correlated with a distance matrix of diatom community data with BEST analysis (Clarke 1993). The model that best explained the variation in diatom communities contained 2 variables, TotQ and Qvarhist ($\rho = 0.463$, $p = 0.01$). Canonical correspondence analysis of all environmental variables produced similar results (data not shown).

TABLE 3. Correlation coefficients of selected physical and chemical variables considered in our study. Mean values were used when correlating water-quality variables to maximum annual discharge/minimum annual discharge for the 1990–2008 time period (Qvarhist) and stream length. See Table 2 for variable descriptions. SRP = soluble reactive P, * = $p < 0.05$, ** = $p < 0.005$.

Environmental variable	TotQ	Qvarhist	Stream length
Qvarhist	0.11	–	0.90**
NO_3	0.06	0.13	0
NH_4	0	0	0.10
SRP	0.12	0.20	0.02
Si	0.33**	0.61	0.37
Na	0.22*	0.91*	0.61
Cl	0.14	0.97**	0.95**
Mg	0.24*	0.94**	0.82*

Different streams had different sized diatoms. Based on the relative abundance counts and estimated biovolumes for each diatom species, a diatom relative biovolume measurement was calculated for each sample. Overall, a significant negative relationship between diatom relative biovolume and average annual stream flow explained 86% of the variability in diatom relative biovolume ($p = 0.004$; Fig. 5A). In general, the relative abundances of small diatoms increased with increasing total annual discharge (Fig. 5B). One species in particular, *Psammothidium* sp. #1, increased exponentially with increasing stream flow ($p < 0.0001$). Analysis of variance results indicate that diatom relative biovolume differed significantly among streams ($p < 0.0001$). Most streams had characteristic ranges of diatom relative biovolumes. Green Creek was an exception and had much more variable diatom sample biovolumes that were significantly correlated with stream flow ($R^2 = 0.61$, $p = 0.04$). These biovolume estimates assume that all diatoms have the same depth, so these estimates probably underestimate diatom relative biovolume, particularly in streams containing larger diatoms. Thus, with more detailed biovolume measurements, the negative slope of the relationship between diatom biovolume and total annual discharge would be expected to increase.

Diatom community composition across streams

NMDS analysis was used to determine stream-scale and temporal variation in diatom community composition. Each stream had a characteristic diatom

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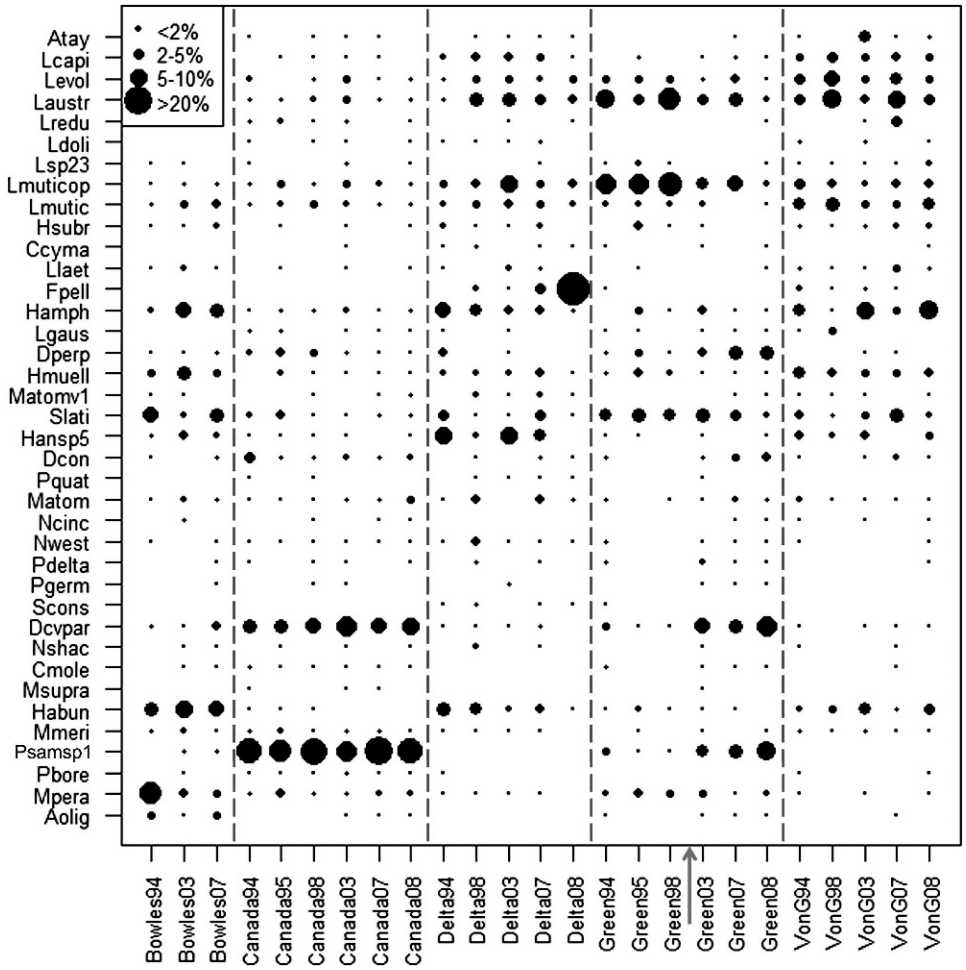


FIG. 4. Dot blot representation of diatom relative abundance counts. Dashed lines separate counts data by stream. The distinctive shift in diatom community composition in Green Creek following the 2001/2002 flood season is marked with an arrow. Streams are coded by name and the last 2 digits of the sampling year. VonG = Von Guerard, Atay = *Achnanthes taylorensis*, Aolig = *Amphora oligotraphenta*, Ccyma = *Chamaepinnularia cymatopleura*, Cmole = *Craticula molestiformis*, Dcon = *Diadesmis contenta*, Dcvpar = *Diadesmis contenta* v. *parallela*, Dperp = *Diadesmis perpusilla*, Fpell = *Fistulifera pelliculosa*, Habun = *Hantzschia abundans*, Hamph = *Hantzschia amphioxys*, Hansp5 = *Hantzschia* sp. #5, Hsubr = *Hantzschia subrupestris*, Hmuell = *Hantzschia amphioxys* f. *muelleri*, Laustr = *Luticola austroatlantica*, Lgaus = *Luticola gaussi*, Llaet = *Luticola laeta*, Lmutic = *Luticola mutica*, Lmuticop = *Luticola muticopsis*, Lcapi = *Luticola muticopsis* f. *capitata*, Levol = *Luticola muticopsis* f. *evoluta*, Lredu = *Luticola muticopsis* f. *reducta*, Ldoli = *Luticola dolia*, Lsp23 = *Luticola* spp. #2/3, Matom = *Mayamaea atomus*, Matomv1 = *Mayamaea atomus* v. #1, Mmeri = *Muelleria meridionalis*, Mpera = *Muelleria peraustralis*, Msupra = *Muelleria supra*, Ncinc = *Navicula cincta*, Nshac = *Navicula shackletoni*, Nwest = *Nitzschia westii*, Pbore = *Pinnularia borealis*, Pdelta = *Pinnularia deltaica*, Pquat = *Pinnularia quaternaria*, Pgerm = *Psammothidium germanii*, Psamsp1 = *Psammothidium* sp. #1, Slati = *Stauroneis latistauros*, Scons = *Stauronella constricta*.

community that broadly distinguished it from its neighbors (Fig. 6A). Von Guerard and Delta Streams clustered more tightly with each other than other streams. Canada Stream points were farthest from the other streams on NMDS axis 1. Green Creek diatom communities were distributed across the 1st axis, indicating higher interannual variability. Bowles and Green Creeks were the closest geographically and most similar in source and stream characteristics, but their diatom communities did not cluster together. PERMANOVA results showed significant differences in diatom communities among most streams except when comparing Delta Stream to Von Guerard Stream or Bowles Creek (Table 4).

Along NMDS axis 1, samples separated based on the relative abundances of *Psammothidium* sp. #1 and *Diadesmis* spp. on the left vs *Hantzschia* and *Luticola* species on the right. *Fistulifera pelliculosa* separated a Delta Stream sample collected during the 2007/2008 season from samples containing *Hantzschia* and *Luticola* species along axis 2 (Figs 4, 6B). Clear grouping of species by genus also occurred.

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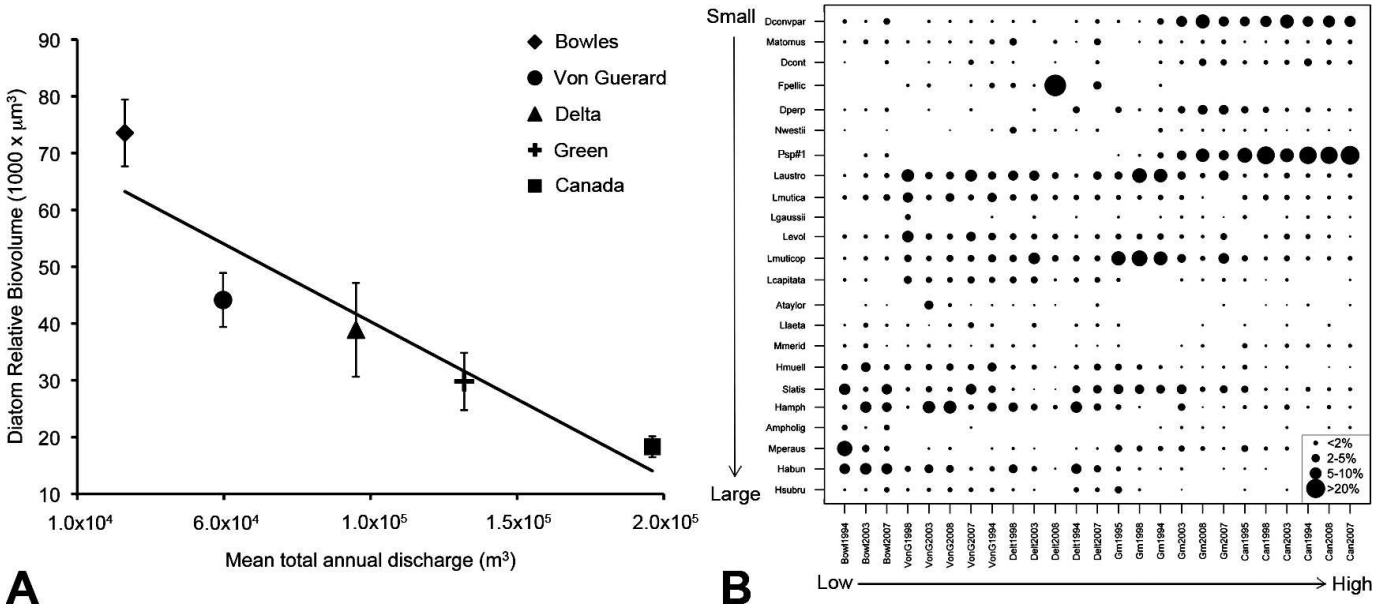


FIG. 5. A.—Mean diatom relative biovolume vs mean total annual discharge for each stream ($R^2 = 0.86$). Mean discharge is based on the continuous flow record between 1990/1991 and 2007/2008, excluding 1992/1993 and 2000/2001, in which data are incomplete. B.—Dot blot representation of diatom relative abundances for common species (≥5%). Samples are arranged by stream along the *x*-axis from lowest to highest total annual discharge. Species are arranged along the *y*-axis from smallest to largest biovolume. See Fig. 4 for diatom abbreviations.

Diatom species richness varied spatially and temporally (Table 5). Canada Stream had the highest mean diatom richness of 27.7 species, whereas the other streams had similar richness values of ~25 species, but these differences were not significant. Significant differences arose when examining species diversity and evenness. Von Guerard Stream had the highest SW diversity and evenness values. These values were significantly higher than values for Canada Stream, which had the lowest values because of the dominance of *Psammothidium* sp. #1. Delta Stream generally had high evenness, but variability was high because of the dominance of *F. pelliculosa* during the 2007/2008 season. Green and Bowles Creeks had similar SW diversity and evenness values throughout the study period.

Microbial-mat responses to a discrete flood event

During the cooling trend in the late 1990s, Chl-*a* concentrations in algal mats generally increased in Delta Stream, Green Creek, and Bowles Creek and decreased in Von Guerard and Canada Streams (Fig. 7A, B). In the most extreme example, during the 2000/2001 season, no flow occurred at the Von Guerard site and no orange mats were visible (DMM, personal observation; Fig. 7A, C). A similar pattern was observed for AFDM (Fig. 7C, D).

Following the flood of 2002/2003, Chl-*a* and AFDM concentrations decreased for all streams. Overall, average Chl-*a* values for all streams dropped from 10.48 to 3.97 µg/cm, and average AFDM values decreased from 13.3 to 4.0 mg/cm. Chl-*a* and AFDM values of algal mats from Canada Stream and Green Creek were only slightly lower after the flood, whereas Chl-*a* and AFDM in Delta Stream and Bowles Creek decreased drastically (Fig. 7A–D). Chl-*a* values declined again in the 2006/2007 season in Green and Bowles Creeks and then rebounded in 2007/2008. AFDM values increased slowly in all streams, and all streams except Bowles Creek returned to preflood values by the 2007/2008 season. No mats were visible in Von Guerard Stream during the season leading up to the flood, but the increase in Chl-*a* values between 2002/2003 and 2007/2008 was similar to the pattern observed in the other streams.

The significant decreases in algal-mat biomass did not correspond with major changes in diatom diversity metrics (Table 5). Nonetheless, SW diversity generally increased in less variable streams, particularly high-flow streams, after the flood. In contrast, increases in SW diversity were minimal in the highly variable Von Guerard and Delta Streams. The same pattern occurred when comparing richness and evenness values. Richness and evenness increased in higher-flow, less-variable streams after the flood,

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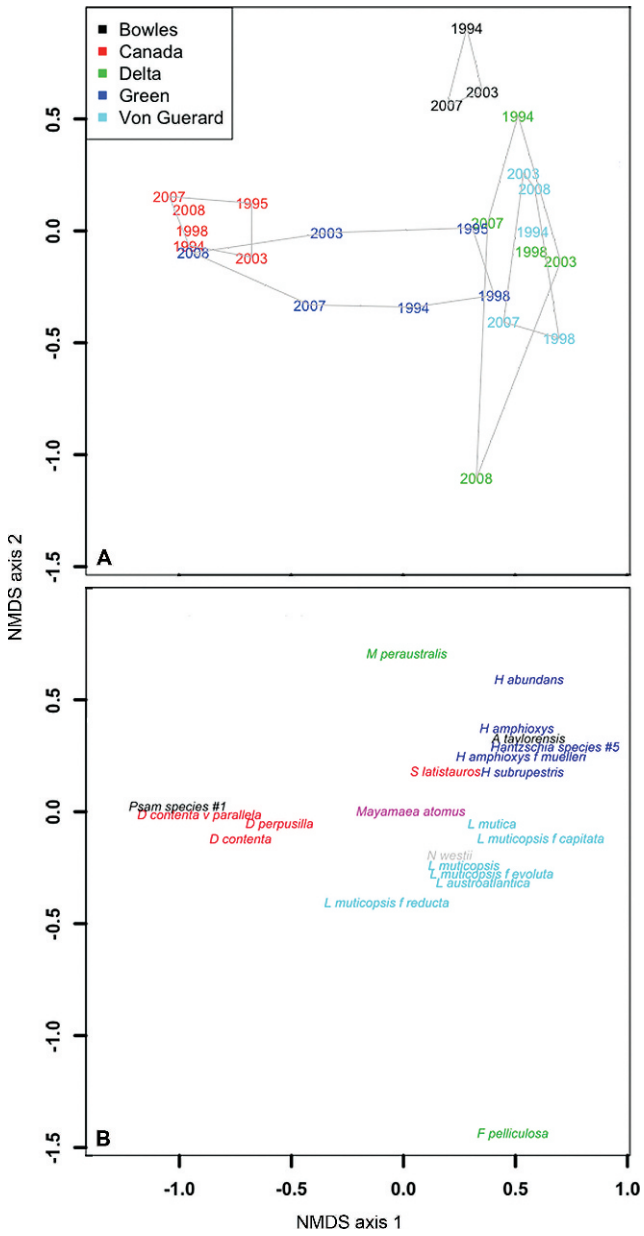


FIG. 6. Nonmetric multidimensional scaling (NMDS) of diatom communities (stress = 0.064) showing plots for sample coordinates (A) and diatom species with relative abundances ≥5% (B) displayed at the centers of their distributions. All species with relative abundances ≥1% were included in the ordination. The distance matrix was calculated based on the Bray–Curtis algorithm. Symbols are color-coded based on stream.

whereas essentially no change in these metrics was observed in more variable streams.

Species responses to the flood varied according to stream (Fig. 4). Relative abundances of *L. muticopsis* and *Hantzschia* sp. #5 temporarily increased in Delta Stream mats after the flood and had returned to preflood levels by 2006/2007. Von Guerard Stream experienced a temporary spike in the relatively rare species *Achnanthes taylorensis*, a decrease in *Luticola* spp., and an increase in *Hantzschia abundans* and *Hantzschia amphioxys*. Green Creek had the most striking changes in species abundance after the flood. Numerous *Luticola* species decreased, and the smaller species *Psammothidium* sp. #1 and *Diadesmis contenta* var *parallela* increased.

Unlike in the other streams, the community changes in Green Creek seem to have persisted after the flood. Hierarchical cluster analysis of the diatom community distance matrix showed Green Creek clustering with Delta Stream and Von Guerard Stream before the flood and clustering with Canada Stream after the flood (Fig. 8A). Our analysis is based on a single sample at each transect for each time period, so a more detailed analysis of Green Creek and Canada Stream was carried out with numerous replicate samples. Cluster analysis of diatom communities from these 2 streams showed that, with the exception of a single sample collected in 2008, Green Creek samples collected before the flood formed a distinct cluster, whereas samples collected after the flood clustered with Canada Stream (Fig. 8B). PERMANOVA results showed that season exerted a significant influence on diatom community composition in Green Creek ($p = 0.004$, $n = 15$), but not in Canada Stream ($p = 0.29$, $n = 18$). Diatom communities in Canada Stream did not vary as much as those in Green Creek, and the most different communities were found during a cold, low-flow season in 2000/2001 rather than after the flood (Fig. 8B).

Discussion

Hydrologic conditions can directly and indirectly influence stream ecosystems. Results of studies conducted in the Antarctic and elsewhere showed that benthic algal communities were more influenced by hydrologic regime than by changes in nutrient pools (Howard-Williams et al. 1986, Riseng et al. 2004). Furthermore, Dry Valley stream algal mats do not appear to be limited by N and P availability (Howard-Williams and Vincent 1989). Our results show that both total annual discharge and historical variation in discharge influence diatom community composition in Dry Valley streams. These variables or related variants are included in the 12 flow-related criteria used for the harshness index developed by Fritz and Dodds (2005) and for the simpler 6-variable harshness index adopted for Dry Valley streams (Esposito et al. 2006). In our study, 2 hydrologic variables were able to sufficiently explain diatom community dynamics in Dry Valley streams and may be important in other meltwater-driven streams that

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TABLE 4. PERMANOVA results testing for differences in diatom communities between streams. Statistically significant correlations ($p < 0.05$) are highlighted in bold.

Stream	Canada	Delta	Green	Von Guerard
Bowles	**0.009**	0.054	**0.018**	**0.020**
Canada		**0.005**	**0.006**	**0.004**
Delta			**0.004**	0.334
Green				**0.005**

lack vegetation, such as those found in polar and high alpine regions.

Significant decreases in algal-mat biomass in all 5 streams after the 2001/2002 flood indicate algal-mat scouring (Fig. 7A–D). This disturbance temporarily altered mat biomass in all streams, despite differences in patterns of change in mat biomass before the flood. The different responses to low flows could reflect small-scale variations in channel morphology. In Bowles Creek, orange microbial mats are restricted to a narrow region within the main channel and probably remained inundated during the low-flow period, and as a result, biomass increased. In streams where mat biomass decreased, the mats are distributed throughout wider channels that would have been more likely to dry. Therefore, the flood appears to have been a large enough disturbance to overwhelm reach-scale differences in stream-channel morphology and drive a common response of reducing biomass.

Despite evidence of algal-mat scouring, most diatom communities returned to their preflood composition after the flood (Fig. 4), a result suggesting that they are resilient to floods. Analysis of only 1 sample for each time period could have influenced these results. However, the lack of interannual variation within a stream (Fig. 6A, B) suggests that the chosen samples represent actual differences in diatom communities across streams. Given the finding that hydrology influences community composition, the ability of diatom communities to rebound following the flood also could be linked to the hydrologic regime. For example, based on analyses of diatom community composition in all 5 streams and on a replicated data set, Green Creek appears to harbor the least resilient communities. Green Creek is unique in that it has an intermediate mean total annual discharge and low historical variation in discharge. In contrast, diatom communities from streams with higher historical variation in discharge and either high or low total annual discharge returned to predisturbance conditions after the flood (Fig. 8A, B). A possible explanation of this finding is that higher magnitude disturbances (e.g., streams with high historical variation in discharge or high or low annual average flow) would select for species that are better adapted to surviving under severe drying or flooding.

The McMurdo Dry Valleys are unique habitats in which to study fundamental ecological processes because of their relatively simple ecosystems and lack of anthropogenic inputs. As a result, great potential exists to test fundamental ecological concepts that can help us to understand more-complex ecosystems. Diatoms are used regularly as ecological indicators because of their sensitivity to environmental changes. However, the mechanisms governing species responses to specific environmental drivers are not always known. Here we have identified size as a potentially important trait influencing the distribution of diatoms in Dry Valley streams (Fig. 5A). Diatoms exhibit distinct size ranges, and this trait is documented for nearly all described species, so its importance can be tested in other stream ecosystems.

The ecological importance of the relationship between diatom relative biovolume and stream flow remains to be elucidated. Other investigators have found a relationship between diatom size and total

TABLE 5. Diatom richness, Shannon–Wiener diversity, and evenness metrics for algal-mat samples from the available flow seasons. Mean values were calculated with data from seasons in which samples were collected from all streams. Postflood (2002/2003 season) values were not significantly different from mean values. Pairwise comparisons of mean diversity metrics for each stream were done with Student's *t*-tests on all seasons for which data were available for both streams. Results of significance tests are represented with lettered superscripts: streams with different letters had significantly different ($p < 0.05$) values for that metric.

Stream	Mean richness	2002/2003 richness	Mean diversity	2002/2003 diversity	Mean evenness	2002/2003 evenness
Bowles	24.3[a]	26	2.40[a,b]	2.53	0.75[a,b,c]	0.78
Canada	27.7[a]	32	1.96[a]	2.31	0.59[a]	0.67
Delta	25.3[a]	25	2.52[a,b]	2.37	0.78[a,b,c]	0.74
Green	24.7[a]	28	2.39[a]	2.60	0.75[b]	0.78
Von Guerard	25.7[a]	25	2.61[b]	2.56	0.81[c]	0.80

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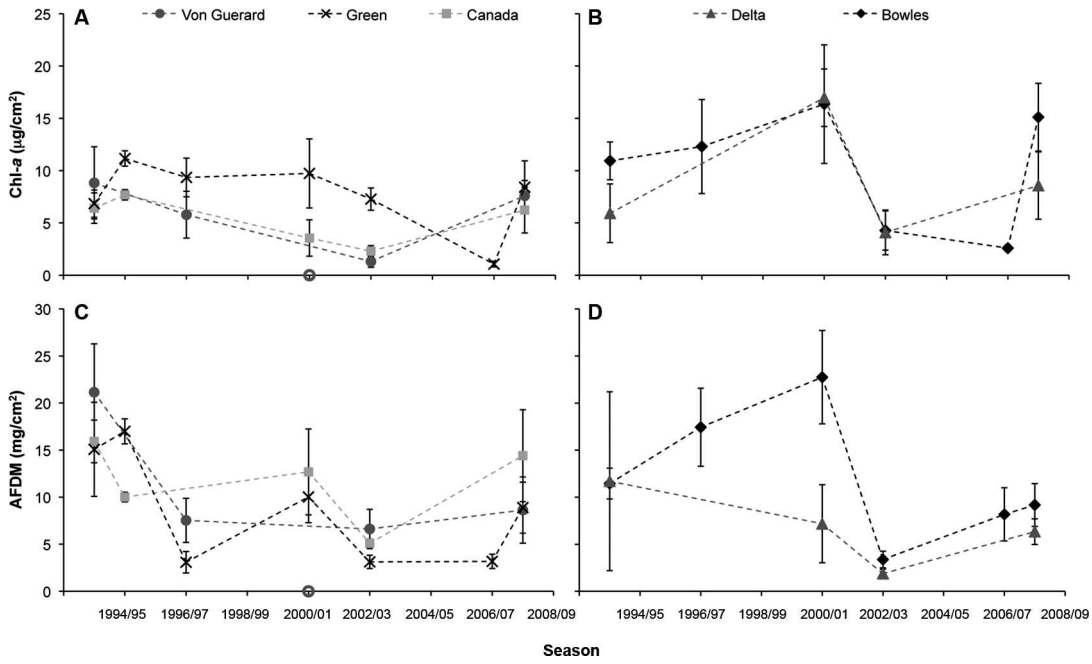


FIG. 7. Interannual variation in algal-mat chlorophyll *a* (Chl-*a*) in Von Guerard Stream, Green Creek, and Canada Stream (A) and in Delta Stream and Bowles Creek (B) and ash-free dry mass (AFDM) in Von Guerard Stream, Green Creek, and Canada Stream (C) and in Delta Stream and Bowles Creek (D). Open circles indicate the lack of orange algal mats in Von Guerard stream during the 2000/2001 season, in which no flow was observed at the transect. Additional biomass data were obtained from the McMurdo Dry Valleys Long-Term Ecological Research (MCMLTER) database.

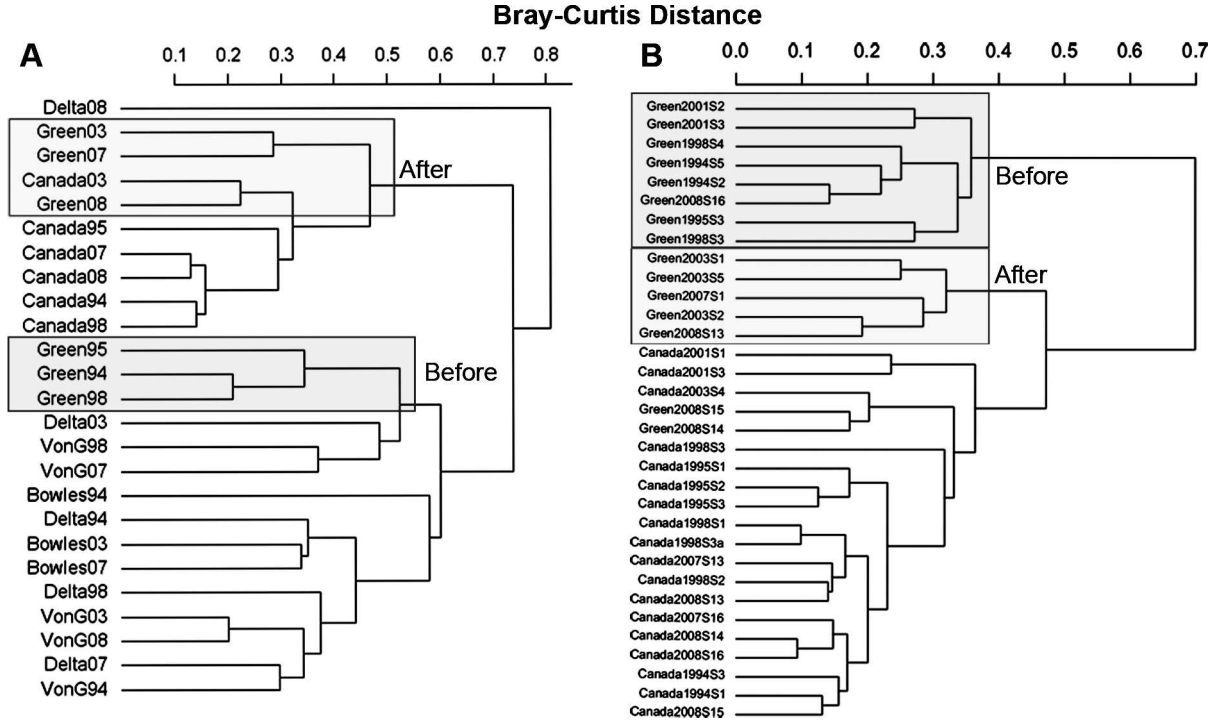


FIG. 8. Dendrograms resulting from hierarchical cluster analyses of diatom community data from all 5 Dry Valley streams (A) and Canada Stream and Green Creek with all replicates included (B). Boxes highlight the clusters containing Green Creek samples before and after the flood event. Labels are written as stream name followed by the sampling year in panel A and as stream name followed by the sampling year and sample number in panel B. VonG = Von Guerard.

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stream P concentrations (Cattaneo et al. 1997), which may be a result of the higher surface area-to-volume ratio of smaller cells (Lavoie et al. 2006). We found no relationship between diatom relative biovolume and SRP, which is not surprising given the relatively small gradient in SRP concentrations in the study streams. Algal mats were growing on the same type of rock-pavement habitat. Thus, the effect of mat type or general habitat characteristics was controlled. However, we cannot rule out the importance of fine-scale spatial variation, e.g., substrate size, in structuring diatom community size or composition. Therefore, the correlation between diatom relative biovolume and total annual discharge may be caused by preferences for a certain substrate particle size (Luce et al. 2010) or physiological factors, such as growth rate, growth form (adnate vs prostrate), or the ability to grow heterotrophically (Admiraal and Peletier 1979). Additional field- and experiment-based studies are needed to determine the mechanism controlling this relationship.

Major ion chemistry could have influenced diatom community structure indirectly because it is strongly correlated to discharge and stream length. Si, in particular, may have acted as an important limiting nutrient, especially given that Si concentrations were generally lower than in temperate streams (Johnson et al. 1969, Wang and Evans 1969, Conley 1997), and streams with lower Si also had smaller diatoms (Table 3, Fig. 5A, B), a result suggesting a connection between diatom size and Si availability. However, Si availability to diatoms in the algal mats may be greater than indicated by ambient stream-water concentrations. The algal mats grow on rapidly weathering streambed alluvium (Maurice et al. 2002), which may provide a steady supply of Si. The potential for Si limitation also can be investigated based on the relationships between nutrients and discharge variables. Si and other conservative ions (e.g., Na and Cl) are correlated with a variety of discharge metrics, whereas N and SRP are not correlated with these metrics (Table 3). If Si were a limiting nutrient, we would expect the relationship between Si and discharge to break down relative to other conservative ions, as it does for N and SRP.

Given the lack of ecological divergence across Dry Valley stream diatom taxa—nearly all belong to the raphid, pennate group, and most belong to aerophilic or subaerophilic genera (Kellogg 1980, van Kerckvoorde 2000, Verleyen et al. 2003, Lowe 2007)—the apparent habitat preferences of diatom genera (Fig. 6B) are probably the result of subtle differences in species traits. Diatom size and motility are among the measured traits that may contribute to the observed ecological preferences.

In the higher-flow streams, *Psammothidium* sp. #1 and *Diadesmis* spp. may have dominated because of their small size, which may enable efficient resource uptake and faster growth rates (Passy 2008) under the low nutrient conditions present in Canada Stream and Green Creek. The genus *Diadesmis* also can form chains, a trait that has been proposed as an adaptation to flow inundation or to aid in the uptake of nutrients (Mayama and Idei 2009). Both genera also occur in other aerophilic and subaerophilic habitats across Antarctica, a distribution suggesting that they are habitat generalists (Spaulding et al. 1997, Ohtsuka ?show=[to]?>et al. 2006, Vinocur and Maidana 2010). In the hydrologically variable Von Guerard and Delta Streams, the small, cosmopolitan species *F. pelliculosa* can become abundant (Fig. 5B). *Fistulifera pelliculosa* appears to be mobilized from upstream ponds and playas and deposited onto mats during intermittent high flows (LFS, unpublished data). This proposed origin is consistent with its occasional presence in high abundances in the longest streams where numerous upstream ponds occur. Overall, the dominance of small species greatly influenced sample evenness, a result suggesting increased probability of local extinctions for uncommon and rare species in these habitats.

Many of the regularly occurring diatoms in Dry Valley algal mats are currently considered Antarctic endemics and, therefore, may harbor unique adaptations to the harsh stream conditions and dynamic hydrologic regime (Esposito et al. 2008). Geographic isolation and climate changes on millennial time scales have allowed extensive radiation of endemic species in the Antarctic (Taton et al. 2003, Pugh and Convey 2008). Recent sampling efforts have yielded dozens of new species and have rapidly expanded our understanding of diatom diversity and biogeography in the Antarctic region (Esposito et al. 2008, Van de Vijver and Mataloni 2008, Van de Vijver et al. 2010, Zidarova et al. 2010).

The importance of species radiation within Antarctic habitats is particularly evident in the genera *Luticola* and *Hantzschia*. Nearly ¼ of all Dry Valley stream diatom species are of the genus *Luticola* (some of these species were described from the Antarctic region and 6 are considered endemic) making it the most diverse genus in Dry Valley streams (West and West 1911, Carlson 1913, Esposito et al. 2008). NMDS results clearly show that the distribution of this genus is not random (Fig. 6B). *Luticola* species often occurred together and were more abundant in highly variable, low-discharge streams than in other stream types. This finding is consistent with their presence in soil and moss environments (Van de Vijver and Mataloni 2008). However, certain species of *Luticola* also reached high relative abundances in higher-discharge Green Creek,

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a result indicating that local adaptations may have occurred within the genus.

The 2nd-most diverse group in Dry Valley streams is the genus *Hantzschia,* with 5 known species and 2 putative endemics. The genus *Hantzschia* has highly mobile representatives and prefers moist or intermittently wetted habitats common in low-flow streams (Round et al. 1990, Zidarova et al. 2010). Consistent with these observations, in Dry Valley streams, *Hantzschia* species grow in similar habitats and prefer the lower-flow environments found in Bowles Creek, Delta Stream, and Von Guerard Stream. The ability of *Hantzschia* species to migrate throughout the mat could allow them to regulate the moisture content of the surrounding environment, thereby conferring protection from desiccation during cold, dry periods. Thus, the previous finding of higher relative abundances of endemic diatoms in more harsh streams (Esposito et al. 2006) may primarily reflect the relative abundances of *Luticola* and *Hantzschia* species, which are well adapted to hydrologically variable, low-flow environments.

Therefore, our results indicate that diatom species diversity and community composition are influenced by hydrologic factors. Understanding ecological controls on stream diatom communities is important for reconstructing past climate (Jones 1996) and for predicting future ecosystem changes. Lakes can typically be used to reconstruct past climate by examining changes in diatom communities throughout a sediment core, but Dry Valley lakes have perennial ice cover and their sediment records are difficult to interpret because of stochastic inputs of aeolian deposits from the surface ice (Spaulding et al. 1997). Diatoms in relict algal mats from perched deltas may provide an additional record for characterizing ecosystem structure under past climate regimes (Kellogg et al. 1980). Furthermore, even though climate studies have concluded that warming is likely in the future (Bracegirdle et al. 2008), the complex and poorly understood nature of climate drivers in the eastern Antarctic makes it difficult to predict climate change for this region (Steig et al. 2009). The opportunity exists to integrate our current understanding of diatom ecology with climate reconstructions based on paleodiatom records to develop a comprehensive model for monitoring ecosystem responses to climate change in this region.

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