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ORIGINAL PAPER

Thermal autecology describes the occurrence patterns of four benthic diatoms in McMurdo Dry Valley streams

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Abstract Benthic microbial mats in the glacial-fed meltwater streams are hotspots of productivity in the McMurdo Dry Valleys (MDV), Antarctica. Benthic diatoms are common in these mats and the >45 primarily endemic taxa represent the most diverse group of eukaryotes in the MDV. In this harsh polar desert, streams are thermally dynamic with daily water temperatures varying 6–9 °C and daily maximum temperatures as high as 15 °C. Stream temperature may play a role in determining growth rates and survival strategies. To understand taxon-specific adaptations to their environment, we measured the growth rates of unialgal cultures of four diatom taxa (*Psammothidium papilio*, *Hantzschia abundans*, *Hantzschia amphioxys*, and *Hantzschia amphioxys* f. *muelleri*) under three temperature conditions (7.6, 10, and 15 °C) that were representative of maximum daily stream temperatures. We found that *P. papilio* exhibited a constant growth rate across the full temperature range; this species is most common in streams that begin to flow early in the summer and with less variable thermal regimes. Growth rates for *H. abundans* were greatest at 15 °C, but showed a non-linear relationship with temperature. *H. amphioxys* f. *muelleri* grew faster than the other taxa studied and thrived at 10 °C. *Hantzschia amphioxys* grew only at the two lower temperatures. These results aligned with the observed relationships between each taxon's relative abundance and stream temperatures in the long-term record maintained by the MDV Long-Term Ecological Research program. Overall, our observations suggest that differences in thermal optima may be one factor contributing to and maintaining the diversity of benthic diatom flora in the MDV.

Keywords Polar diatoms · Growth rate · Temperature · In vivo fluorescence · Antarctica · Long-Term Ecological Research (LTER)

Introduction

Diatoms are common in extreme polar environments characterized by low temperatures, many months of darkness, varying day length, and potentially high solar irradiance (Hoover and Pikuta 2010; Spaulding et al. 2010). In glacier-fed streams in the McMurdo Dry Valleys (MDV) in Antarctica, diatoms are common in benthic microbial mats and represent the most diverse group of eukaryotic organisms in the region. Diatoms are commonly used as ecological indicators because of their sensitivity to environmental conditions and specific tolerances to abiotic and biotic fluctuations (Smol and Stoermer 2010). Thus, the use of diatoms for environmental monitoring and reconstruction in Polar Regions, such as the MDV, depends upon a detailed knowledge of their autecology.

Temperature is among the most important environmental factors in determining growth rates and survival of microorganisms (Madigan et al. 2009) and is an important aspect of algal ecology and physiology (Raven and Geider

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1988). The survival of phototrophic organisms in Antarctica requires the coordination of the temperature-independent process of light absorption with the temperature-dependent production of energy-containing organic molecules, such as ATP and NADPH (Morgan-Kiss et al. 2006). Benthic diatoms in MDV streams can experience a consistent state of energy imbalance due to high irradiance and low temperatures. In these habitats, low temperatures represent a dominant physiological constraint on primary productivity (Hawes and Howard-Williams 1998). Many of the resident diatoms likely employ a complex suite of biochemical traits to carry out photosynthesis in cold habitats (Morgan-Kiss et al. 2006; Cvetkovska et al. 2016) and can be classified as either psychrotrophs (tolerate cold temperatures) or psychrophiles (require cold temperatures). Psychrotrophs can maintain growth at temperatures <15 °C, exhibit optimal growth at temperatures >15 °C, and have upper survival limits ≥20 °C, whereas psychrophiles exhibit optimal growth at temperatures <15 °C and require temperatures ≤20 °C for survival (Morita 1975).

In polar regions, several studies have investigated the temperature growth response of psychrophilic diatoms and highlight the importance of temperature as an environmental filter (Fiala and Oriol 1990; Longhi et al. 2003; Karsten et al. 2006). For example, Antarctic benthic marine diatoms isolated from the South Shetland Islands and grown in culture were found to have growth optima at 0 °C with an upper survival limit of 7 °C for *Gyrosigma subsalinum* var. *antarctica* Frenguelli and Orlando and 9 °C for *Odontella litigiosa* (Van Heurck) Hoban (Longhi et al. 2003). While these studies focused on diatoms in marine and frozen seawater habitats, they more generally demonstrated how specialized taxa with psychrophilic adaptations can survive, and even thrive, in persistent low-temperature conditions. We expect that similar investigations into the temperature growth responses of MDV diatoms will provide insight into the types of taxon-specific adaptations that allow these organisms to persist in such extreme habitats.

Considering the sensitivity of diatom growth rates to temperature (Admiraal 1976; Montagnes and Franklin 2001; Butterwick et al. 2004), the distribution of taxa and variation in community composition can often be linked to variation in thermal environments (Patrick 1948; Patrick and Reimer 1966; Suzuki and Takahashi 1995; Weckstrom et al. 1997). Seaburg et al. (1981) showed that two MDV diatom taxa occupied different thermal niches based on different tolerances when grown in a range of temperatures. Such findings suggest that interspecific differences in temperature-dependent growth rates may explain some heterogeneity in the abundances and distribution of benthic diatom taxa across MDV streams.

Flow regime is known to be the primary abiotic control on diatom communities in MDV streams, where flora become dominated by endemic taxa during periods of intermittent and low stream flow (Esposito et al. 2006; Stanish et al. 2011, 2012; Kohler et al. 2015). Although a stream's thermal characteristics are primarily determined by daily changes in solar radiation (see Fig. A1 in Online Resource 1), flow regime can have a modulating influence (Conovitz et al. 1998; Cozzetto et al. 2006). During midsummer, the stream temperatures are typically 4–6 °C when the sun is low on the horizon, and then increase to 10–15 °C when the sun is directly overhead. The higher peak daily temperatures of 15 °C occur in shallow streams at low flow on cloudless days (Cozzetto et al. 2006). As the flow increases and/or water depth increases, as is typical of shorter streams with narrower channels, peak daily temperatures may only reach 10 °C (Cozzetto et al. 2006). No study to date has explored the potential link between the thermal characteristics of MDV streams and diatom community composition using diatom thermal niche preferences. Such an understanding may be relevant for using diatoms as ecological indicators (e.g., in sediment records, Konfirst et al. 2011).

The four benthic diatom taxa examined in this study are frequently observed in MDV streams and occupy different microbial mat habitat types with varying abundances. *Psammothidium papilio* (Kellogg et al.) Kopalova and Van de Vijver is the most common in orange-colored mats, which are formed by *Oscillatoria* and *Phormidium* cyanophytes that grow in the stream thalweg and stay submerged during low flow (Kohler et al. 2015). The isolates of the aerophilic *Hantzschia* taxa used in this study, *Hantzschia abundans* (Lange-Bertalot), *Hantzschia amphioxys* (Ehrenberg) Grunow, and *Hantzschia amphioxys* f. *muelleri* (Ehrenberg) Ko-Bayashi, are more frequently observed in black mats composed of the cyanobacterium *Nostoc*. Black mats grow at the stream margins with fewer days of submersion (Alger et al. 1997; Kohler et al. 2015). Diel melt pulses control when marginal black mats are submerged by stream flow and exposed to in-stream temperatures, in addition to inter- and intra-seasonal variability in flow regimes (Kohler et al. 2015).

Here we focus on the temperature growth preferences of four common diatoms found in microbial mats in MDV streams to provide more information toward understanding how benthic diatom autecological strategies can contribute to regional biodiversity. Given the relatively cold temperatures of MDV streams (maximum temperatures only reaching 8–15 °C), we expected that some of the diatom taxa would exhibit optimal growth at <15 °C and thus be categorized as psychrophilic. Further, we hypothesized that MDV stream diatoms would exhibit differences in temperature optima and that such differences in taxon-specific thermal preferences could promote niche partitioning among resident taxa in MDV streams. Therefore, variation in thermal regimes across streams in the MDV landscape could be a contributing factor to the relatively high diversity observed for benthic diatoms in the region. We tested our hypothesis with two approaches. First, we measured the growth rates of cultured diatoms over a range of temperatures representative of the maximum daily temperatures typically reached in different MDV streams: 7.6, 10, and 15 °C (Cozzetto et al. 2006). These temperatures broadly reflect the stream temperature maxima when conditions are most suitable for balancing temperature-independent and temperature-dependent components of photosynthesis, and thus growth is most efficient. Second, we assessed empirical relationships between diatom relative abundances and stream environmental data collected as part of the MDV Long-Term Ecological Research (MCM LTER) program to determine if there is evidence that stream temperature influences diatom community composition across the MDV landscape. Results from both approaches taken together provided evidence that diatom species growth rates and distributions are linked to variation in thermal regimes across streams.

Materials and methods

Site description

The diatoms examined in this study were harvested from microbial mats in the glacial-fed streams in the MDV (Fig. 1), which cover 4500 km^2 (Levy 2013) and represent the largest ice-free area in Antarctica. Data collected in the MDV and reported in this study have been archived as part of the MCM LTER program (mcm.lternet.edu). Starting in 1990, stream flow measurements have been recorded for streams in the Lake Fryxell Basin in Taylor Valley. At <10 cm year^{-1}, annual precipitation in the MDV is negligible (Doran et al. 2002). Most precipitation falls as snow during winter though the rate of sublimation exceeds accumulation (Fountain et al. 2009). During the austral summer, there is continuous light and air temperatures may reach 10 °C in some places (Doran et al. 2002). During the winter months, darkness and extreme cold loom over the landscape. The biological communities in the MDV are limited to groups of microbes, mosses, lichens, and few invertebrates and are present in the soils, lakes, ephemeral streams, and glacial surfaces (Adams et al. 2006).

For 4–10 weeks during the summer, well-established stream channels are fed by glacial meltwater. These streams are a primary link between source glaciers and the perennially ice-covered lakes at the valley floors (Conovitz et al. 1998). Streams can support abundant microbial mats attached to streambed substrata (McKnight and Tate 1995). These mats are tolerant of both cold and highly variable temperatures (Seaburg et al. 1981; Tang et al. 1997), as well as unsteady flow, periodic desiccation, and intense solar radiation. In mid-summer, maximum daily stream temperatures range from 8 to 15 °C and are affected by stream discharge and net radiation patterns (Cozzetto et al. 2006). Stream temperatures typically exhibit diel fluctuations of 6–9 °C, reaching minimum temperatures as low as 0.1 °C (von Guerard et al. 1995; Cozzetto et al. 2006). Due to evaporative and convective constraints, maximum temperatures do not exceed 15 °C (Cozzetto et al. 2006) (Table 1, also see Fig. A2 in Online Resource 1).

Culture method and experimental design

Freshwater pennate diatom taxa (Fig. 2) were isolated from benthic microbial mats in MDV streams and cultivated as unialgal but xenic stock cultures. Stock cultures were established by isolating taxonomic strains within a laminar flow hood using a serial dilution method and sterile equipment. No additional methods were taken to eliminate bacteria or other contaminants because there is a lack of information on how such sterilization and subsequent removal of potential bacterial symbionts (Stanish et al. 2013) would affect the growth of diatom cultures from this region of Antarctica (Hünken et al. 2008; Amin et al. 2012).

Isolated strains of *P. papilio*, *H. abundans*, *H. amphioxys*, and *H. amphioxys* f. *muelleri* (Table 2) were identified from cleaned burn mounts following descriptions in Esposito et al. (2008), Zidarova et al. (2010), and Kopalová (2012) and the Antarctic Freshwater Diatoms database (http://huey.colorado.edu/diatoms/about/index.php) using a compound light microscope at ×1250 magnification (Olympus Vanox). In an effort to maintain accurate taxonomy of diatom culture strains, close attention was attributed to the different morphological features between *H. amphioxys* and *H. amphioxys* f. *muelleri* by following Esposito et al. (2008), where *H. amphioxys* f. *muelleri* is constricted in valve length and has strongly capitate apices and finer striae density compared to *H. amphioxys* (Fig. 2). We focused on these taxa because they have been regularly observed with varying abundances in many Dry Valley streams (Fig. 3, Esposito et al. 2006; Stanish et al. 2011, 2012), with different distributions ranging from endemic to globally widespread. Two of the *Hantzschia* species, *H. amphioxys* and *H. abundans*, are currently described as globally widespread (Esposito et al. 2008). Conversely, *P. papilio* is reported endemic to continental Antarctica (Sabbe et al. 2003; Esposito et al. 2008) and the Maritime Antarctic Region (Zidarova 2008; Kopalová 2012). Similarly, *H. amphioxys* f. *muelleri* is

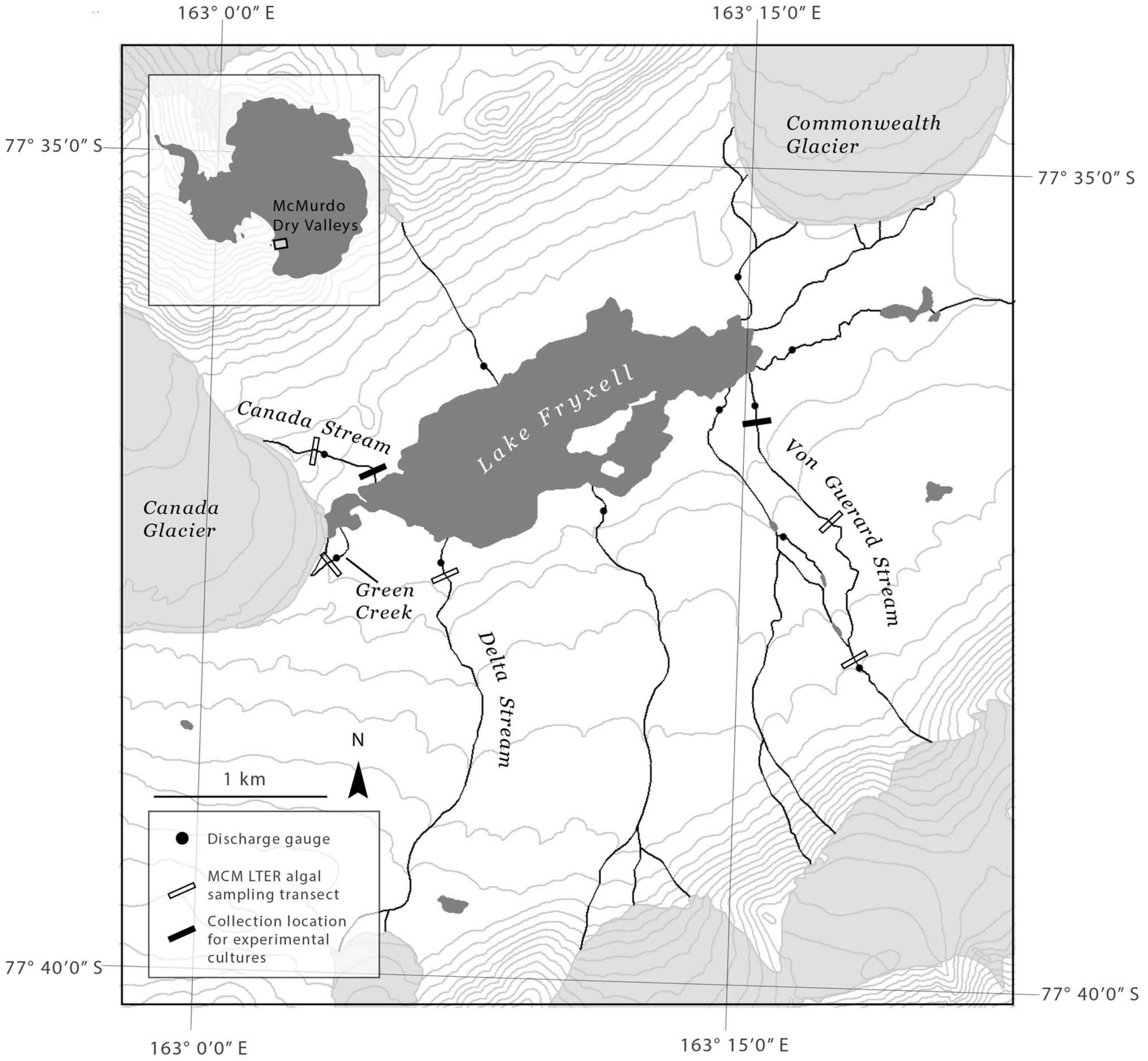

Fig. 1 Reference map of Lake Fryxell Basin in Lower Taylor Valley of the McMurdo Dry Valleys (MDV), Antarctica. Stream discharge gauge sites are indicated by circles. The McMurdo Dry Valleys Long-Term Ecological Research program (MCM LTER) algal sampling transects for the four streams examined in this study are marked with *open rectangles*. *Solid rectangles* indicate where the stock cultures used in the growth experiments were harvested in Canada Stream and Von Guerard Stream

endemic to continental Antarctica (Ko-Bayashi 1965; Esposito et al. 2008) the maritime Antarctic region (Zidarova et al. 2010), while also observed in Patagonia (Müller 1909). Specimens of *H. amphioxys* f. *muelleri* from continental Antarctica that are found in the MDV are constricted in size (33–44 µm) compared to strains from the maritime Antarctic region of Livingston Island (40–55 µm) (Zidarova et al. 2010).

Stock cultures of the four isolated species were incubated in circumneutral (pH 6.8) DY-V growth medium (Andersen 2005) in 10-mL glass culture vessels, and maintained in a growth chamber at 7.6 °C with a 12:12 h light:dark cycle. Illumination was focused from above with two cool white fluorescent lamps and an irradiance of 40 µmol photons m^{-2} s^{-1}. This light regime was used to mimic daily net radiation in the Dry Valleys (see Fig. A1 in Online Resource 1). Despite 24-h sunlight during the austral summer, the duration of direct solar radiation on benthic microbial mats in streams is not continuous and cycles on a diurnal basis, in part due to a low solar angle and mountain shadows on either side of the valley (Conovitz et al. 1998). Stock cultures were maintained with

Table 1 Stream characteristics for four streams in Fryxell Basin arranged from low to high (left to right) stream flow intermittence and stream water temperatures

Stream	Canada	Green	Delta	Von Guerard
Average season length (days)^{a}	71	57	55	44
Average annual discharge (m^{3} year^{-1})^{a,c}	2.06×10^{5}	1.42×10^{5}	1.05×10^{5}	5.97×10^{4}
Average maximum water temperatures (°C)^{b,c}	7–10	9–12	10–12	10–12
Magnitude of daily temperature range (°C)^{b,c}	3–8	8–11	7–11	6–11
Stream flow intermittency ranking (1 = least intermittent, 4 = most intermittent)^{d}	1	2	3	4

Values derived from (a) Stanish et al. (2011), (b) Cozzetto et al. (2006), (c) von Guerard et al. (1995), and (d) Stanish et al. (2012), in addition to limited unpublished temperature data taken periodically from MCM LTER stream measurements

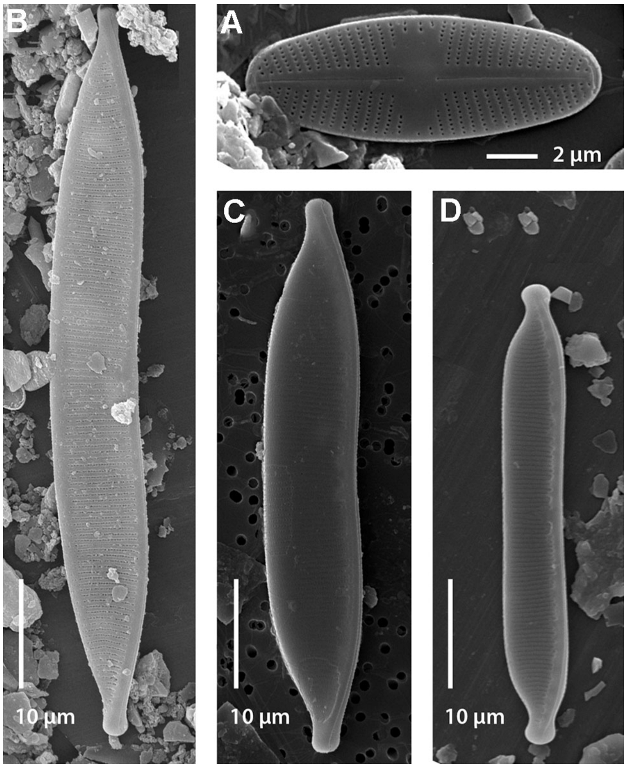

Fig. 2 Scanning electron micrographs of benthic diatoms isolated from microbial mats in streams in Lake Fryxell Basin, including **a** *Psammothidium papilio,* **b** *Hantzschia abundans,* **c** *Hantzschia amphioxys*, and **d** *Hantzschia amphioxys* f. *muelleri*. SEMs provided by Kateřina Kopalová and Bart Van de Vijver

subcultures, and the health of subculture strains was assessed by noting any morphological abnormalities and examining the sizes of chloroplasts.

For each temperature experiment, batches of test cultures were prepared from stock material. Approximately 30 live cells were aseptically isolated from stock cultures and inoculated into 8-mL borosilicate cuvette test tubes with 7-mL DY-V medium using drawn Pasteur pipettes and microscopy (Nikon Eclipse TS100). Throughout the experimental incubation, the test cultures were replete with DY-V medium to maintain a 7 mL medium volume. Cultures were grown under the same conditions as stock cultures, but in separate growth chambers depending on the temperatures tested: 7.6, 10, and 15 °C.

At minimum, four replicate cultures for each of the taxa were independently incubated in each treatment. Several taxa, however, had a greater number of replicate cultures cultivated. At 7.6 °C, 19 replicate cultures of *P. papilio* were grown over three years, six replicate cultures of *H. abundans* were grown over two years, and nine replicate cultures of *H. amphioxys* f. *muelleri* were grown over 3 years. At 10 °C, seven replicate cultures of *H. amphioxys* f. *muelleri* were grown over two consecutive years. At 15 °C, four replicate cultures were grown for each taxon. We used a one-way ANOVA to test for significant changes in growth rates among trial years for each taxon.

Growth measurements

We assessed how intrinsic growth rate, which is the population growth rate that occurs when density dependence does not limit growth (Gotelli 2001), varied across cultures raised in the different temperature treatments. We expected to observe logistic growth in each culture, where intrinsic growth occurs during the exponential growth phase of a logistic growth curve. Logistic growth curves also include lag and stationary phases, which are periods of zero growth that precede and follow the exponential growth phase, respectively. We focused on intrinsic growth because many unknowns influence the lag phase of cultures inoculated with low cell concentrations as cells adjust to their environment (Yates and Smotzer 2007).

Due to the slow growth rates and tendency of these diatoms to adhere to surfaces, an in vivo fluorometric method was used to determine and monitor growth rates in a non-damaging manner (Karsten et al. 1996). Diatom growth was measured as the increase in chlorophyll *a* fluorescence over time in cultures grown in test tubes. We assumed that chlorophyll *a* density did not change within cells during the course of the experiment, and thus changes in fluorescence were proportional to diatom population

Table 2 Taxa cultivated in the present study with noted distributions and original description references

Taxon	Length (µm)	Distribution	Reference
Psammothidium papilio	10–17	Antarctic Continent and Maritime Antarctic Region endemic	(Kellogg et al.) Kopalova et al. 2012
Hantzschia abundans	49–94	Globally widespread	Lange-Bertalot (1993)
Hantzschia amphioxys	27–61	Globally widespread	(Ehrenberg) Grunow (1880)
Hantzschia amphioxys f. *muelleri*	33–44	Antarctic Continent, Maritime Antarctic Region, and Patagonia endemic	(Ehrenberg) Ko-Bayashi (1965)

growth rates. Chlorophyll *a* fluorescence was recorded with a Turner Designs Model 10-000R field fluorometer (Turner Designs, Mountain View, CA). Fluorescence measurements were performed 4–5 times per week and carried out during the same time each day until a cessation in growth was observed. Three replicate fluorescence readings were measured for each culture and averaged for that day. Blanks containing only DY-V medium were measured prior to culture tubes and subtracted from culture fluorescence values.

We calculated intrinsic growth for each culture by fitting an exponential growth curve to changes in chlorophyll *a* fluorescence over time, such that

$$N_t = N_0 e^{\mu t}, \tag{1}$$

where N_0 is the initial fluorescence value, N_t is the measured fluorescence at a given day, μ is the intrinsic growth rate (day^{-1}) during the exponential growth phase, and t is the elapsed time in days. Population doubling time was calculated as

$$T_2 = \frac{1}{\mu}. \tag{2}$$

For each temperature treatment, the mean values of μ and T_2 were calculated from replicate culture groups. A one-way ANOVA was used to test for a difference in mean division rates among temperature treatments for each cultivated taxon. Similarly, a one-way ANOVA was used to test for a difference in mean division rates among incubation runs that occurred over several years for each taxon–temperature combination. Tukey's honest significant difference (HSD) test was used to determine where differences occurred among groups. We also examined differences in the duration of the exponential growth phase among taxa and temperature treatments.

Empirical models to explain variation in diatom relative abundances

We assessed whether information about the thermal characteristics of streams improved our ability to explain observed temporal and spatial variation in taxon relative abundances (RAs). We used the records of diatom counts from orange and black benthic mats in stream channels (Fig. 1), stream temperature data, and stream flow data collected during 1994–2013 and archived by the MCM LTER (http://mcm.lternet.edu/). We used linear mixed effects (LME) models (Venables and Ripley 2002; Zuur et al. 2009, 2010) and tested if models including measures of stream thermal properties more accurately predicted RAs of each taxon than models without temperature data.

LME models were constructed using the nlme (Pinheiro et al. 2017) and MASS (Venables and Ripley 2002) packages for R (R Core Team 2016) to predict RAs for each of the four diatom taxa examined in the growth studies. For each taxon, we only included records where RAs were >0 because we assumed that the variation in non-zero RAs can be attributed to the variation in diatom growth performance among sites, whereas presence/absence data may have many more underlying causes that are beyond the scope of this study (e.g., sampling effort, priority effects, biogeographic history, etc.). Distributions of diatom RAs were log-normal for all taxa except *P. papilio*, which exhibited a normal distribution after an arcsine square root transformation. RAs were transformed accordingly (McCune and Grace 2002) and used as the response variables in the LME models. The data set included RAs of the four diatom taxa in four streams in Taylor Valley (Canada, Green, Delta, and Von Guerard) from 1994 to 2015. We used *stream* nested within *year* as a random intercept term to account for autocorrelation among observations grouped within a stream and within a season. We used LMEs with only random factors as null models. We used two-way stepwise selection to add fixed factors and two-way interactions based on stream intermittency ranking (*intermitt_rank*) from Stanish et al. (2012) to capture among-stream differences in hydrologic history, the number of flow days during the season antecedent to sampling date (*flowdays*), and the type of mat from which a sample was collected (*mat_type*; two categories: orange or black). Fixed factors and interaction terms were excluded from the model if they had a variance inflation factor >10 (Fox and Weisberg 2010). The best fit models constructed from these variables were considered

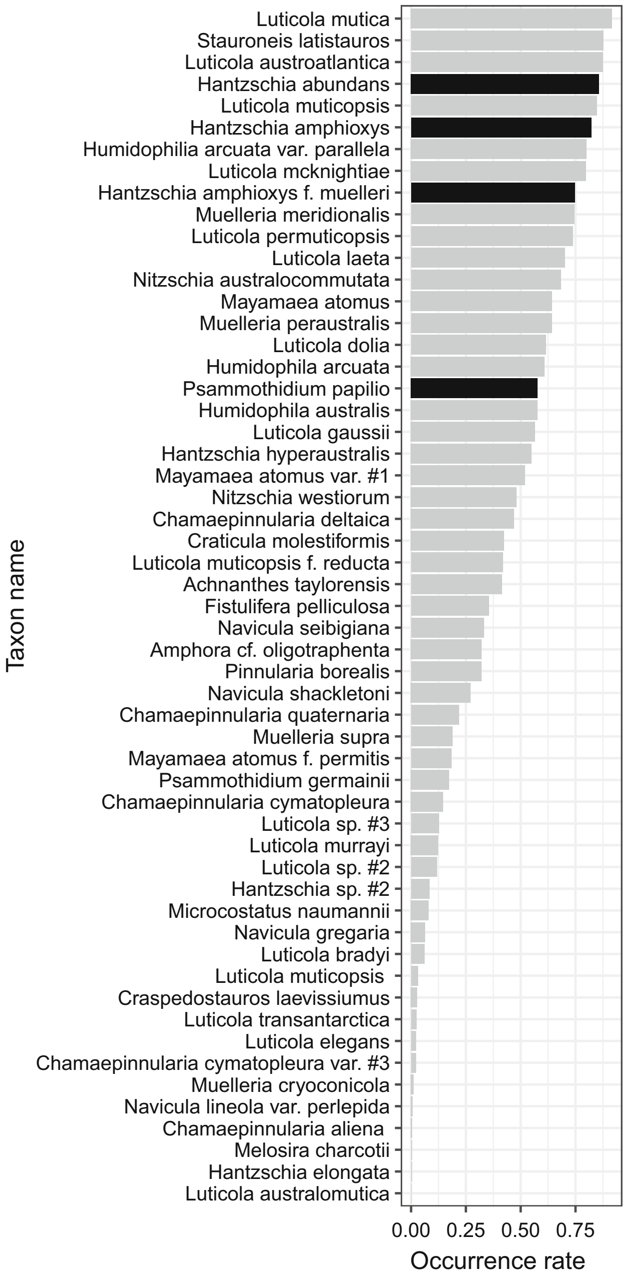

Fig. 3 Rank occurrence of diatom taxa in 575 samples collected from streams in the McMurdo Dry Valleys as part of the MCM LTER project. Data are archived in the Antarctic Freshwater Diatom Database. *Bars* representing the occurrences of taxa used in this study are *shaded black*

“base models” because they represented fixed factors that have been shown to influence diatom distributions in the past studies. Base model significance was tested against null models using a log-likelihood ratio test (Venables and Ripley 2002).

We then used two-way stepwise selection to add fixed factors describing stream thermal characteristics (please see Table A2 in Online Resource 1) to the base models. Candidate variables included measures of stream temperature at time of sampling; measures of 5th, 50th, and 95th percentile temperatures and variation in stream temperature for one season antecedent to the sample date; measures of 5th, 50th, and 95th percentile temperatures and variation in stream temperature for the entire record (1994–2015); and measures of cumulative thermal input (degree days above freezing [DDAF] and counts of days above 7.6 and 10 °C). The resultant best fit temperature models included the base model plus any temperature variables that increased model fit significantly when compared against the base model using a log-likelihood ratio test. We used marginal coefficients of determination (R^2_{m}) and conditional coefficients of determination (R^2_{c}) to quantify the amount of variation explained by fixed factors and the total model, respectively (Nakagawa and Schielzeth 2013; Barton 2015).

Results

Growth rates

In each temperature treatment, diatom cultures displayed logistic growth curves, except for *H. amphioxys*, which did not grow at 15 °C (e.g., see Fig. 4 for representative growth curves from the 10 °C treatment). The mean duration of the lag phases was not consistent (see Table A3 in Online Resource 1) among replicate treatment/taxon combinations; however, the duration of exponential growth and the observed growth rates were consistent among replicate temperature experiments. Overall, the four taxa demonstrated slow intrinsic growth in the three temperature treatments relative to other published values on polar (Fiala and Oriol 1990; Longhi et al. 2003; Souffreau et al. 2013) and temperate (Admiraal 1976; Gilstad and Sakshaug 1990; Butterwick et al. 2004; Kutlu and Buyukisik 2011; Souffreau et al. 2013) diatoms. Observed mean intrinsic growth rates were between 0.05 and 0.18 day^{-1} (Table 3), and the standard deviations in growth rate for the temperature treatments were relatively low, ranging from ±0.003 to ±0.03.

For *P. papilio,* the average intrinsic growth rate at each temperature remained near 0.10 day^{-1}, corresponding to a doubling time of 9.5–10 days, and cultures showed no statistical difference in growth rates among the three treatments ($F_{2,24} = 0.064$, $p = 0.938$, Table 3; Fig. 5a). The average time that cultures were in their exponential growth phase lasted approximately 18–23 days across temperature treatments. Among the three 7.6 °C trials, the exponential phase lasted 18, 23, and 25 days; at 10 °C the mean exponential phase lasted 23 days; and at 15 °C the exponential phase lasted 22 days.

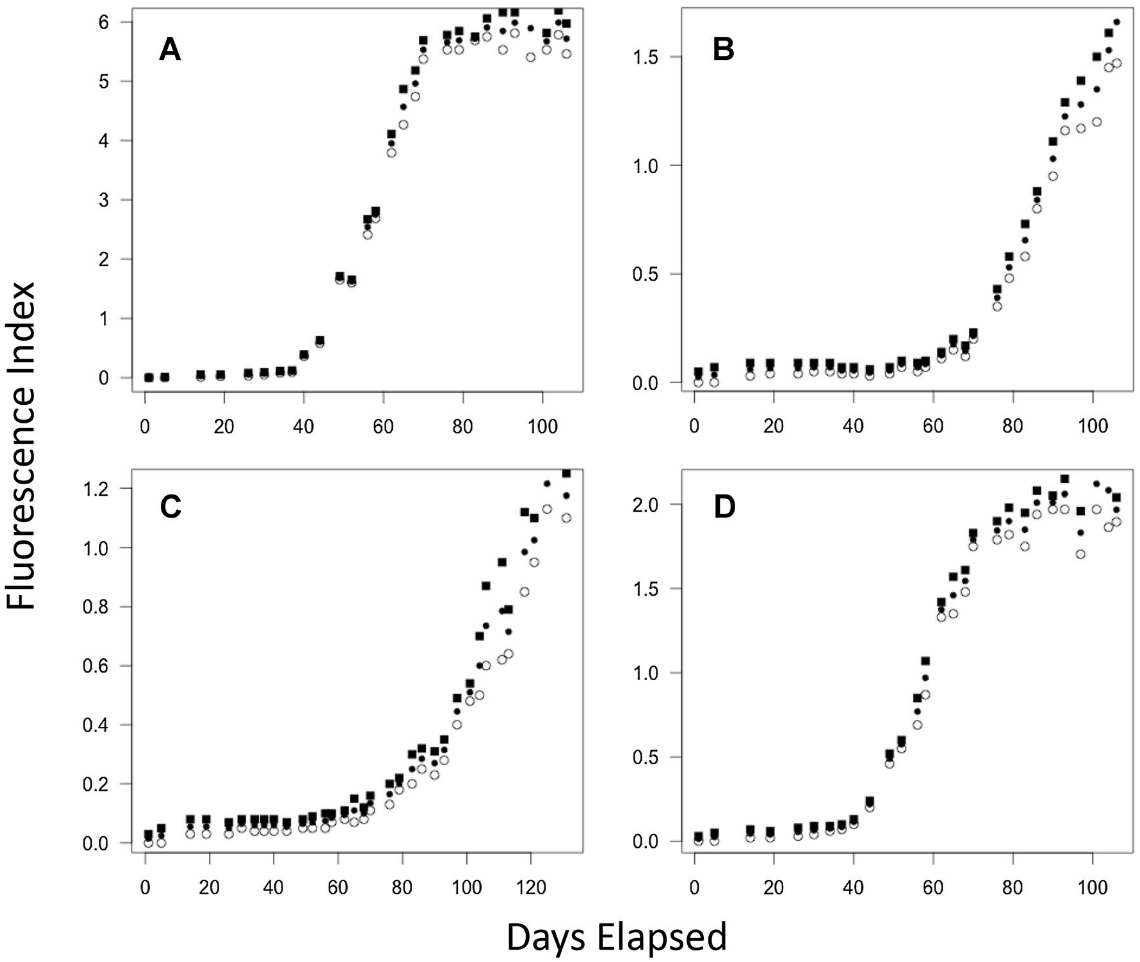

Fig. 4 Representative logistic growth curves for selected diatom cultures grown at 10 °C with three replicate fluorescence readings shown (distinguished by symbol type) for **a** *Psammothidium papilio*, **b** *Hantzschia abundans*, **c** *Hantzschia amphioxys*, and **d** *Hantzschia amphioxys* f. *muelleri*. Intrinsic growth rates were calculated from the fluorescence values measured during the exponential growth phase

Table 3 Observed growth rates for benthic diatoms that were cultured from streams in Lake Fryxell Basin and grown under different temperatures

Taxon	Temperature treatments								
	7.6 °C			10 °C			15 °C		
	μ	T_2	n	μ	T_2	n	μ	T_2	n
Psammothidium papilio	0.10 (±0.02)	10.1 (±2.03)	19	0.10 (±0.007)	9.7 (±0.71)	4	0.11 (±0.01)	9.5 (±1.56)	4
Hantzschia abundans	0.088 (±0.01)	11.4 (±1.5)	6	0.071 (±0.01)	14.2 (±2.8)	4	0.11 (±0.01)	9.5 (±0.85)	4
Hantzschia amphioxys	0.07 (±0.008)	14 (±1.7)	4	0.05 (±0.003)	19.8 (±1.4)	4	NA	NA	4
Hantzschia amphioxys f. *muelleri*	0.13 (±0.01)	7.5 (±0.9)	9	0.18 (±0.03)	5.8 (±0.98)	7	0.12 (±0.02)	7.3 (±1.25)	4

Growth rates (μ) are reported as mean (±SD) divisions day^{-1}, T_2 = mean doubling time (±SD) in days, n = sample size

NA indicates no available data because no growth was observed

In contrast, growth rates varied among temperature treatments for *Hantzschia* taxa. *Hantzschia. abundans* showed a significant growth response to temperature treatments ($F_{2,11} = 7.60$, $p = 0.008$, Table 3; Fig. 5b), with its fastest growth rate (mean ± SD = 0.11 ± 0.01 day^{-1}, $n = 4$) at the warmest incubation temperature (15 °C). At 7.6 °C, the mean growth rate was 0.09 ± 0.01 day^{-1} ($n = 6$) and growth rates were not different between trial years ($F_{1,4} = 0.013$, $p = 0.910$). At 10 °C, the mean growth rate of replicate cultures was

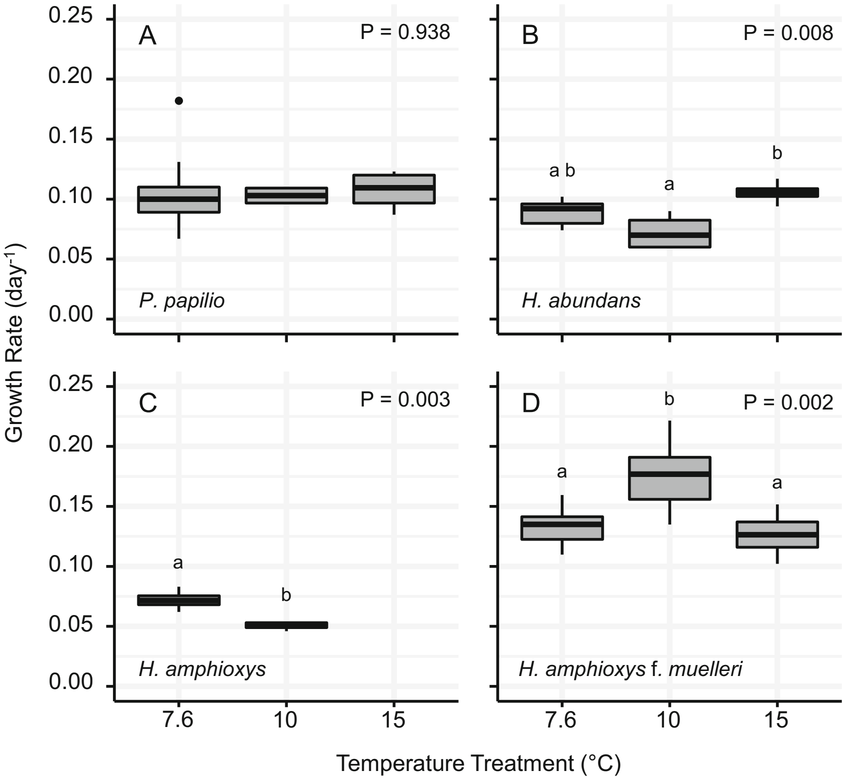

Fig. 5 Box plots showing the range of growth rates for cultivated Antarctic diatoms at three temperatures. *Horizontal black bars* indicate the median growth rate among cultures for each temperature treatment for **a** *Psammothidium papilio,* **b** *Hantzschia abundans*, **c** *Hantzschia amphioxys,* and **d** *Hantzschia amphioxys* f. *muelleri*. Differences among temperatures were tested with a one-way ANOVA. Tukey's post hoc pair-wise comparisons are shown, with different letters indicating significant differences in growth rates for a taxon based on a critical value of $p < 0.05$

0.07 ± 0.01 day^{-1} ($n = 4$). Mean doubling times of cultures were 11.4 days at 7.6 °C, 14.2 days at 10 °C, and 9.5 days at 15 °C.

For this taxon, the duration of the exponential growth phase was consistent across temperature experiments ($F_{1,12} = 1.87$, $p = 0.197$), and the duration of the exponential phase (~26 days) did not vary between the two trial years for the 7.6 °C temperature treatment group ($F_{1,4} = 0.137$, $p = 0.73$). The exponential growth phase lasted an average of 32 days at 10 °C and 22 days at 15 °C (each treatment only had one trial year).

The potentially widespread taxon, *H. amphioxys*, revealed the slowest growth rate among the taxa examined in this study (Table 3; Fig. 5c). This taxon exhibited its fastest growth (0.07 ± 0.008 day^{-1}, $n = 4$) at the coldest temperature (7.6 °C). Growth rates were slower ($F_{1,6} = 21.42$, $p = 0.003$) in the 10 °C treatment (0.05 ± 0.003 day^{-1}, $n = 4$) and did not grow in the 15 °C treatment ($n = 4$). The doubling times for this taxon were 14 and 19.8 days at 7.6 and 10 °C, respectively. The doubling times at 10 °C were approximately twice as long as was typically observed for other taxa 10 °C (Table 3).

Although growth rates for *H. amphioxys* were slow, this taxon did exhibit logistic growth curves in the 7.6 and 10 °C treatments, which had lengthy lag and exponential phases (e.g., Fig. 4c). The exponential phase lasted 35.5 days at 7.6 °C and 43 days at 10 °C. The difference in exponential growth between the two temperatures was not significant ($F_{1,6} = 2.147$, $p = 0.193$).

The endemic *H. amphioxys* f. *muelleri* exhibited the fastest growth rates in each temperature treatment. Its intrinsic growth rates were statistically different among treatments ($F_{2,17} = 8.878$, $p = 0.002$), and its optimal growth was 0.18 ± 0.03 day^{-1} ($n = 7$) in the 10 °C treatment. Growth rates were not significantly different among different trial years within the 10 °C treatment ($F_{1,5} = 0.937$, $p = 0.377$). This taxon exhibited a faster growth rate (0.12 ± 0.02 day^{-1}, $n = 4$) at 15 °C than the other taxa. At 7.6 °C, the mean growth rate of was 0.13 ± 0.01 day^{-1} ($n = 9$) and growth rates were not significant between 7.6 °C trial experiments ($F_{2,6} = 2.471$, $p = 0.160$). This taxon exhibited its fastest growth rate at 10 °C, where the mean population doubling time was 5.8 days. At 7.6 °C, the mean doubling time was 7.5 days and at 15 °C the mean doubling time was 7.3 days (Table 3).

Cultures of *H. amphioxys* f. *muelleri* showed similar exponential growth patterns within temperature experiments. The average duration of exponential growth was 19.5 days for replicate 7.6 °C cultures, and the length of the exponential phase did not vary among replicate trial years. At 10 °C, the duration of lag and exponential phases varied among replicated trial years ($F_{1,5} = 77.51$, $p = 0.0003$); the initial experiment had a 22-day mean exponential phase, whereas cultures in the final replicated 10 °C experiment had a mean exponential phase of 7.75 days. At 15 °C, the mean time of exponential growth lasted 14 days among culture tubes.

Factors explaining variation in diatom relative abundances in dry valley streams

In base models, stream intermittency rank, season length (*flowdays*), and mat type explained 61% of the variation in RAs for *P. papilio* and 41–46% of the variation for the three *Hantzschia* taxa (Table 4). Generally, *P. papilio* was more dominant in orange mats in streams with more consistent flow, whereas all three *Hantzschia* taxa were more dominant in black mats than orange mats (Fig. 6). Significant interaction terms for *H. abundans* and *H. amphioxys* f. *muelleri* indicate that the response these taxa showed toward flow intermittency and season length was conditional on mat type (Table 4).

LME models including stream temperature variables created more parsimonious explanations of variation in diatom RAs for all three *Hantzschia* taxa, but not for *P. papilio* (Table 4), and these models increased coefficients of determination by 3–15%. Generally, *Hantzschia* RAs were negatively correlated with seasonal measures of temperature, growing season, and variation in temperature. However, *H. amphioxys* f. *muelleri* showed a weak positive correlation with temperature on the day that samples were collected (see Table A2 in Online Resource 1).

Discussion

Laboratory-controlled temperature growth experiments presented here indicate that stream water temperature may affect growth rates differently for *Psammothidium* and *Hantzschia* taxa in the MDV. We expected that some of the taxa residing in South Victoria Land would exhibit a psychrophilic response with optimal growth in incubations <15 °C. Experimental data supported this prediction for two of the four taxa that were studied. Overall, our observations support the idea that thermal habitat preferences vary among taxa, potentially contributing to diatom diversity through niche separation. We were able to distinguish different growth responses to experimental treatments that were representative of the range of water temperatures that commonly occur among habitats in MDV streams (see Fig. A2 in Online Resource 1, Cozzetto et al. 2006).

Using recorded relative abundance and stream environmental data over a 21-year period, we were able to translate laboratory-based growth rates to predict temperature preferences of natural populations in the field. Our analysis of long-term records of stream temperature and diatom community composition in benthic mats showed that empirical models using stream temperature data better predicted relative abundances for *Hantzschia* taxa than models without temperature data. This outcome indicates that the experimental results are relevant for understanding the distribution of diatoms across MDV streams. Thus, we suggest that the long-term stream temperature record can supplement models based on other physio-chemical predictors of diatom distributions in MDV streams, such as variable discharge (Esposito et al. 2006; Stanish et al. 2011, 2012; Kohler et al. 2015) and available nutrients (Kohler et al. 2016).

Slow growth

We generally observed slower growth than what was reported for other Antarctic diatoms at similar temperatures. We found that *H. amphioxys* grew most slowly and had undetectable growth at the warmest temperature treatment (15 °C). In contrast, a previous study (Souffreau et al. 2013) showed that an Antarctic strain of *H. amphioxys* isolated from the Schirmacher Oasis grew more rapidly, exhibiting optimal growth of 0.25 day^{-1} at 20 °C. However, we observed similar growth rates at lower temperatures (e.g., 7.6 °C). Importantly, Souffreau et al. (2013) demonstrated that Antarctic lineages of globally widespread taxa have slower growth rates in general, and lower optimal growth temperatures compared to their temperate counterparts. Supporting this hypothesis, a temperate strain of *H. amphioxys* isolated from the Izmir bay in the Aegean Sea had a markedly greater optimal growth rate of approximately 1.3 day^{-1} at 18 °C (Kutlu and Buyukisik 2011).

We found that the endemic taxon *H. amphioxys* f. *muelleri* grew the fastest overall and showed optimal growth at 10 °C with a mean division rate of 0.18 day^{-1}. This growth rate is comparable to optimal growth values reported on Antarctic diatoms (e.g., Souffreau et al. 2013); however, still it is much slower compared to temperate diatoms (Butterwick et al. 2004; Kutlu and Buyukisik 2011). The other endemic taxon *P. papilio* showed consistently slow (0.10 day^{-1}) and persistent growth rates that were invariant with temperature. The widespread *H. abundans* isolate had a growth rate similar to *P. papilio* and was distinctive in showing a modest increase in growth at the warmest treatment (15 °C). The generally low growth rates we present can potentially be attributed to other confounding variables of culture environment such as light availability and photoperiod (Raven and Geider 1988) or bacterial interactions in

Table 4 Linear mixed effects models explaining variation in relative abundances for diatom taxa observed in the MCM LTER record in streams in Lake Fryxell Basin, based on stream cyanobacteria mat type, stream flow history, and stream water temperature

Taxon	Model type	df	AIC	Test	*L* ratio	*p* value	R^2_{m}	R^2_{c}	Model terms
Psammothidium papilio	Null model	4	−51.5				0.00	0.62	(1|year/stream)
	Base model	9	−136.7	Null vs base	95.20	<0.0001	0.61	0.73	+mat_type(orange) +flowdays −intermitt_rank +***null model***
	Base model + temp.	11	−136.8	Base vs base + temp	4.11	0.1278	n.s.	n.s.	n.s.
Hantzschia abundans	Null model	4	621.0				0.00	0.47	(1|year/stream)
	Base model	7	566.7	Null vs base	60.32	<0.0001	0.46	0.57	−mat_type(orange) +intermitt_rank +mat_type × intermittent_rank +***null model***
	Base model + temp.	9	560.2	Base vs base + temp	10.43	0.0054	0.49	0.58	−ddaf_stream_mean −temp_var_2seas +***base model***
Hantzschia amphioxys	Null model	4	513.3				0.00	0.38	(1|year/stream)
	Base model	7	457.9	Null vs base	61.48	<0.0001	0.41	0.47	−mat_type(orange) −flowdays +intermitt_rank +***null model***
	Base model + temp.	10	450.0	Base vs base + temp	13.88	0.0031	0.46	0.50	−thresh_mean_7.6 −temp_daily_mean_t5 −temp_var_2seas +***base model***
Hantzschia amphioxys f. *muelleri*	Null model	4	635.0				0.00	0.35	(1|year/stream)
	Base model	8	581.8	Null vs base	61.25	<0.0001	0.41	0.48	+flowdays +intermitt_rank −flowdays × mat_type(orange) −intermitt_rank × mat_type(orange)
	Base model + temp.	11	539.9	Base vs base + temp	27.04	<0.0001	0.56	0.56	−temp_var_2seas −thresh_max_7.6 +temp_mean_sample +***base model***

Relative abundances were log transformed, except for *P. papilio*, which were arcsine square root transformed. All models include a nested random term ~1|year_seas/stream, and null models only include an intercept term and a random term. Base models include best fit predictors based on mat type (orange or black mat), stream intermittency ranking, and flow days for the season in which the sample was collected. Base models were allowed to include significant two-way interactions if they increased fit. Intermittency rank was based on Stanish et al. (2012) rankings, where more intermittent streams have higher numerical rankings: Canada as the least intermittent stream is ranked 1. R^2_{m} is the coefficient of determination for fixed effects and R^2_{c} is the total model coefficient of determination. See Table A1 in Online Resource 1 for descriptions of individual model terms and Table A2 in Online Resource 1 for partial standardized beta weights for fixed factors included in best fit models. Note that n.s. indicates not statistically significant

xenic stock cultures (Hünken et al. 2008). Furthermore, laboratory-based experiments do not necessarily represent temperature growth responses of diatoms in natural habitat. However, in this context, the slow growth rates we observed at natural growth temperatures support the hypothesis that these taxa are not necessarily obligate psychrophiles, but they can tolerate low temperatures despite constraints on primary productivity. Considering the slow growth rates of MDV diatoms, thermal adaptation could be a slow and limited process, especially with short annual growing seasons of 4–10 weeks.

It should be noted that the possibility exists that these diatoms grow faster at temperatures greater than those tested here, particularly for the widespread *H. abundans* isolate, which showed a modest increase in growth at 15 °C. However, growth rates above 15 °C are not

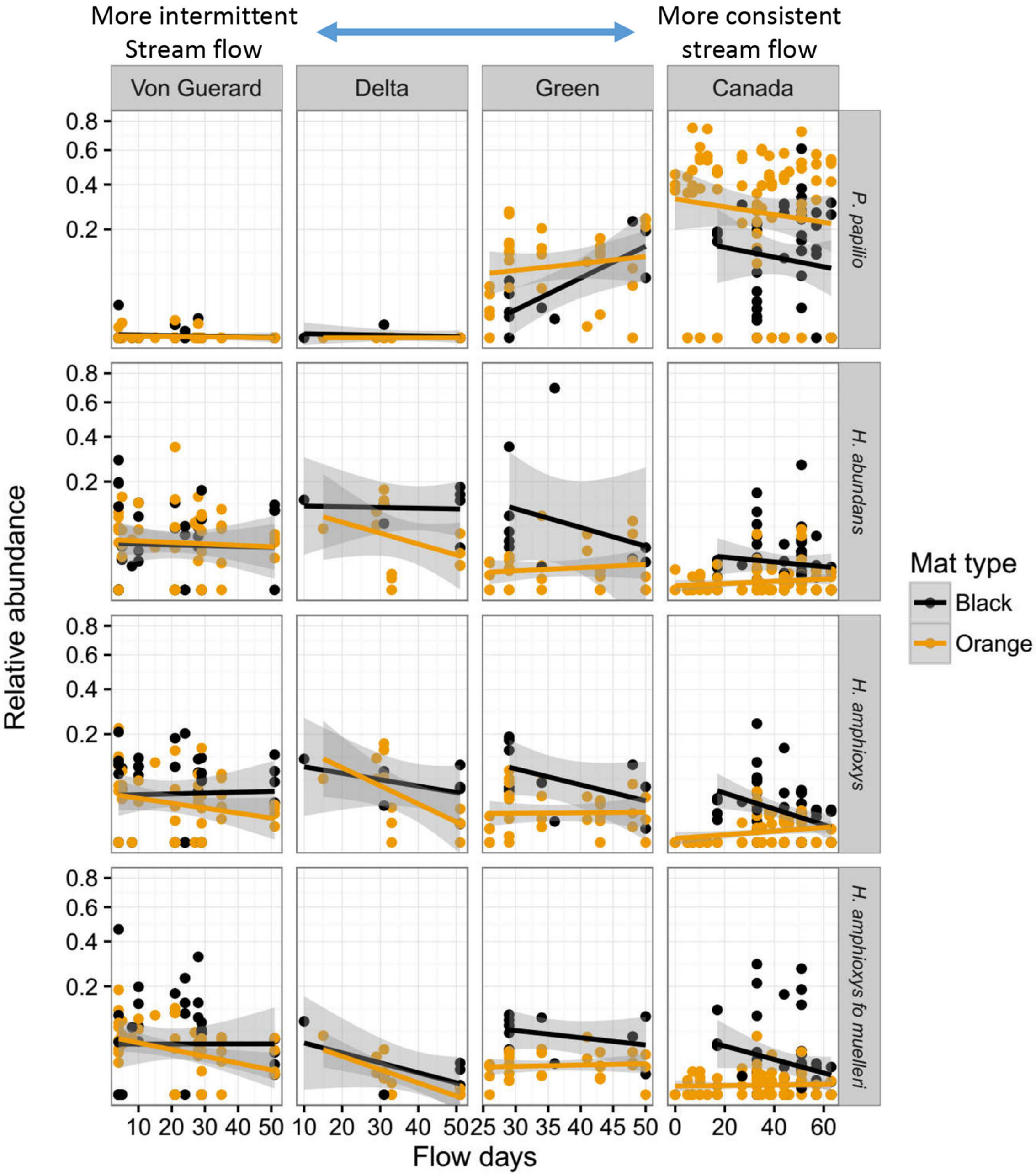

Fig. 6 Relative abundances (RAs) of *Psammothidium papilio*, *Hantzschia abundans*, *Hantzschia amphioxys*, and *Hantzschia amphioxys* f. *muelleri* observed in the two dominant stream mat types (*orange and black*) from the MCM LTER record for four streams in Lake Fryxell Basin. Streams are arranged by flow intermittency ranking (Stanish et al. 2012). Flow days (*x*-axis) indicates the number of days that stream flow had been recorded at a stream gauge during a season prior to the date a diatom sample was collected. See Table 4 for statistical analyses. (Color figure online)

ecologically relevant for these isolates because MDV streams do not exceed that temperature threshold (Cozzetto et al. 2006). The slow growth rates we present imply that these taxa are not necessarily adapted to the low temperatures that are characteristic of their glacial-fed habitat, and they may persist by taking advantage of periods during the day when temperature is more favorable for growth. Overall, the abundance of these taxa in MDV streams demonstrates their ability to tolerate the harsh conditions in the MDV, including a dynamic hydrologic regime (Stanish et al. 2011, 2012) and extreme desiccation and freeze–thaw cycles (Davey 1989; Souffreau et al. 2010).

Psychrophile or psychrotroph

Many studies have reported the psychrophilic growth of marine algae from high latitudes (Fiala and Oriol 1990; Aletsee and Jahnke 1992; Longhi et al. 2003) with psychrophiles being predominantly found in ice-frozen habitats with stable cold temperatures. However, our results on freshwater taxa are generally similar to Seaburg et al. (1981), who found limited evidence of obligatory low-temperature preferences among MDV stream algae. Two of the four diatom taxa we studied can potentially be described as psychrophiles, which exhibit higher growth rates at temperatures below 15 °C (Morita 1975; Morgan-Kiss et al. 2006; Cvetkovska et al. 2016). Optimal growth of *H. amphioxys* f. *muelleri* occurred at 10 °C and exhibited sustained growth at 15 °C; however, the upper survival limit was not resolved in the present study. In contrast, *H. amphioxys* exhibited obligatory psychrophilic growth in a narrow temperature range below 15 °C. These results do not match temperature growth responses reported for other Antarctic lineages of *H. amphioxys*. Souffreau et al. (2013) found different temperature preferences between Antarctic and temperate lineages of *H. amphioxys,* and that Antarctic strains tolerated a wide range of temperatures, from 2.9 to ca. 25 °C, with an optimal growth temperature of 20 °C. One explanation for our contradictory finding is that we observed psychrophilic growth by a cryptic species within the widespread *Hantzschia* complex. Our classification of this taxon as psychrophilic should be viewed with caution, considering the wider temperature growth preferences reported on another Antarctic lineage of this taxon (Souffreau et al. 2013). An alternative explanation is that culture conditions limited our ability to obtain growing populations of *H. amphioxys* at 15 °C, rather than a temperature effect. Thus, further studies on temperature constraints for this strain of *H. amphioxys* should be considered. In addition, molecular evidence and accurate taxonomy are needed to confirm any specific lineage or divergence of the *H. amphioxys* strain we studied.

In glacial-fed stream habitats in the MDV, unstable temperature regimes may allow the persistence of psychrotrophic algae that can survive and grow at low temperatures, but may have optimal growth temperatures >15 °C. The ability of these taxa to survive the harsh environment with long periods of desiccation and seasonal freeze–thaw cycles is presumably more important than psychrophilic adaptations of more efficient growth in in situ habitat temperatures. However, the evolved adaptations to the stream's thermal environment (e.g., results on *H. amphioxys* f. *muelleri*) may provide some benefit to the organism's resilience in the harsh environment. Moreover, the psychrotrophic growth characteristics of *P. papilio* or *H.amphioxys* suggest that these taxa evolved in warmer climates prior to colonizing the MDV and are adapted to warmer temperatures while still resilient to other abiotic stressors of the polar habitat (Seaburg et al. 1981; Tang et al. 1997). Such an understanding of taxon-specific temperature sensitivities can be useful for explaining the heterogeneous community structure of diatoms across thermally variable streams in the MDV.

Thermal preferences and implications for diatom distributions in MDV streams

Similar to previous studies (Esposito et al. 2006; Stanish et al. 2012), the distributional data from the LTER record showed that stream intermittency, growing season length, and mat type explained a substantial proportion of the variation in RAs for all four diatom taxa; however, the three *Hantzschia* were also sensitive to variation in stream thermal regimes. The *Hantzschia* taxa were the most dominant early in the growing season, showed negative relationships with measures of stream temperature, and had higher RAs in streams that were more intermittent. These observations suggest that the *Hantzschia* taxa are potentially cold adapted and more capable of opportunistic growth in the MDV than *P. papilio*. *H. amphioxys* f. *muelleri*, which exhibited psychrophilic tendencies, is likely the most opportunistic taxon of the group. The spatial and temporal distribution of *P. papilio* corroborates our inference from the experimental results that this taxon is a persistent and slow grower at cold temperatures. Thus, *P. papilio* becomes dominant later in the growing season, especially in more stable habitats, such as orange mats.

These results reinforce the findings of previous studies that a broad range of physiological tolerances are needed to take advantage of the seasonal presence of liquid water in the streams flowing in this harsh polar desert (Stanish et al. 2012). The extreme habitat in the MDV has exerted a strong regional environmental filter to select for organisms with broad tolerances that are able to persist in an unstable environment characterized by large physio-chemical fluctuations (sensu Chase 2007), including variable cold temperatures (Vincent and Vincent 1982; Vincent 2000).

Conclusions

By comparing growth experiments with the long-term record from the MCM LTER, we were able to use the autecology of these organisms to better understand their distribution in the MDV landscape. In general, we found evidence that some diatoms found in MDV streams may be psychrophilic or psychrotrophic. *Psammothidium papilio* employs a different strategy to survive the harsh conditions of MDV streams than *Hantzschia* spp. *Psammothidium* *papilio* growth rates were relatively slow, persistent, and invariant with temperature, whereas *Hantzschia* spp. appeared to be better adapted to opportunistic growth in MDV stream habitats. These traits helped explain the differences in the distributional data for *P. papilio* and *Hantzschia* spp. in MDV streams recorded in the MCM LTER data set.

Overall, we found that the growth response of cultured diatoms to temperature translated well to explain the variation in diatom dominance across MDV streams. This study emphasizes that understanding the autecology of diatoms and potentially other indicator taxa, in combination with accurate taxonomic identifications in a long-term record of ecological data, can provide insight into the links between environmental gradients and biodiversity patterns. Such relationships are valuable for understanding the underlying processes that organize contemporary biodiversity patterns (Stanish et al. 2012; Sokol et al. 2013; Kohler et al. 2015; Sakaeva et al. 2016; Kohler et al. 2016), as well as the potential for Antarctic ecosystems to respond in the face of a changing climate (Wall 2007; Turner et al. 2009; Convey et al. 2009).

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