# Consequences of nuisance algal blooms of *Didymosphenia geminata* on invertebrate communities in Rocky Mountain streams

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Abstract: As climate change accelerates, low summer stream flows are becoming increasingly common in the Colorado Rocky Mountains, USA. The diatom Didymosphenia geminata (Lyngb.) M. Schmidt, typically observed under low-flow and low-P conditions, produces nuisance growth-persistent and extensive proliferation, covering the bottoms of streams in thick algal mats. Nuisance blooms of this diatom physically alter the benthic environment and thereby affect freshwater invertebrates directly and indirectly by altering stream food webs. We compared 9 y of survey data (2013-2021) of *D. geminata* proliferation with the composition of the macroinvertebrate communities at 8 stream sites near the Rocky Mountain Biological Laboratory in western Colorado. We counted and identified samples of benthic macroinvertebrates and used a glass-bottomed viewing box to estimate D. geminata biovolume at 2 scales: macrohabitat conditions (site level: 2013-2021) and microhabitat conditions (sample level: 2020-2021). At both scales, increases in D. geminata proliferation were associated with shifts in macroinvertebrate community composition that could be explained by altered abundances of focal taxa, specifically declines in Heptageniidae (Ephemeroptera) and increases in Chironomidae (Diptera). Abundances of Baetidae (Ephemeroptera) were unaffected by increased D. geminata biovolume. These changes indicate degradation of stream habitat for some sensitive groups of macroinvertebrates, which may affect higher trophic levels, such as trout, in these mountain stream ecosystems. As climate change trends toward lower summer streamflow, understanding the effects of proliferation of this ecosystem engineer is key to predicting the impact of climate change on stream food webs.

**Key words:** *Didymosphenia geminata*, didymo, nuisance species, algal blooms, Colorado Rocky Mountains, macroinvertebrate community structure, streams, Heptageniidae, Baetidae, Chironomidae, ecosystem engineers

Increasing evidence shows that anthropogenic climate change increases both frequency and intensity of extreme weather events, causing myriad negative repercussions for ecological and human systems (IPCC et al. 2022). Most climate models predict that climate change will cause higher temperatures and lead to less frequent, more extreme precipitation events, although predictions for the frequency of precipitation events are spatially variable (Aiken and Rauscher 2020, IPCC et al. 2022). In addition, winters are changing, especially affecting high latitude and high elevation ecosystems (Rixen et al. 2022), and extreme events and interannual variability in winter snowfall have important influences on water resources in the western United States (Lute and Abatzoglou 2014).

As a consequence of altered temperatures and precipitation, climate change also affects flow conditions in streams throughout the world (Marx et al. 2018, Gómez-Gener et al. 2020, Rogers et al. 2020). Recent precipitation deficits have reduced the snowpack in mountain ecosystems, which alters quantity and timing of snowmelt and decreases the albedo (diffuse reflectivity) of surrounding areas, thereby increasing evaporation and lowering river flow (Milly and Dunne 2020). Across western North America and specifically in western Colorado, recent studies have documented

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declines in winter snowpack (USEPA 2016, Fyfe et al. 2017, Gil-Alana 2021) and earlier spring snowmelt (Hidalgo et al. 2009) resulting in reduced stream flow (Xiao et al. 2018). More specifically, annual peak stream flows have declined throughout the Colorado River catchment, especially at high elevations (Solander et al. 2017), with complete snow melt occurring earlier in the spring in some areas (Inouye 2022).

Low stream flow can lead to altered biophysical conditions that can, in turn, support the proliferation of nuisance algal blooms, such as those of Didymosphenia geminata (Lyngb.) M. Schmidt (family Bacillariophyceae). Also known as didymo or rock snot, D. geminata is a freshwater diatom that forms mats of mucopolysaccharide stalks, present in fossil records in the Arctic, Asia, Europe, and North America since the last glaciation (Taylor and Bothwell 2014, Spaulding et al. 2020). This species is a natural part of periphyton communities' characteristic of low-nutrient, fastflowing, cold, high-elevation streams (Spaulding and Elwell 2007, Kumar et al. 2009, Bishop and Spaulding 2017) and is native to rivers in the Colorado Rocky Mountains, reported since at least the 1960s (Taylor and Bothwell 2014). This once little-noticed diatom has emerged as a nuisance species since the 1990s in streams across the Holarctic and as an invasive species in more distant regions, including New Zealand (Kilroy and Unwin 2011). Nuisance blooms of this species are characterized by the formation of extracellular polysaccharide stalks and are both temporally persistent and spatially extensive (Spaulding and Elwell 2007).

The relative importance of habitat drivers of D. geminata proliferations are debated (Bergey and Spaulding 2015, Taylor and Bothwell 2015, Bray et al. 2016); but these blooms are unique compared with other diatom blooms in that they occur under oligotrophic conditions, specifically low phosphorous (P), rather than eutrophic conditions (Kilroy and Bothwell 2012). Low P has been considered a key determinant of bloom development (Bothwell et al. 2014), but recent observational and experimental evidence casts doubt on the singular importance of this potential cause of D. geminata proliferation (West et al. 2020). For example, streams in the Upper East River drainage of the Colorado River catchment are both currently and historically P limited (Moslemi 2010, Balik et al. 2021), but nuisance blooms of *D. geminata* appear, anecdotally, to be a relatively recent phenomenon, first observed in the East River in 2006 (BLP, personal observation).

In addition to low P, low streamflow conditions have been associated with *D. geminata* proliferation. For example, this diatom is often abundant downstream of dams and in flow-regulated streams (Kirkwood et al. 2007, 2009) and has been associated with glacial melt recession (Brahney et al. 2021). Low-flow conditions allow *D. geminata* to avoid the shear stresses of extreme high-flow events (flushing or scouring flows), which can be used as a control on *D. geminata* growth (Cullis et al. 2015). *Didymosphenia gemi-* *nata* proliferations also have consequences for near-bed stream flows by increasing shear stress just above the mats and decreasing current velocity within mats (Larned et al. 2011). Therefore, *D. geminata* proliferations have the potential to alter the microhabitats occupied by other benthic organisms, which can shift the relative abundance of macro-invertebrate species (Marshall 2007, Anderson et al. 2014, Larned and Kilroy 2014).

In lotic ecosystems, macroinvertebrates have historically been used as a bioassessment tool to evaluate the quality of aquatic habitats. Macroinvertebrate species are diverse, and there is variability among species in vulnerability to disturbance (Robinson and Minshall 1986, Cairns and Pratt 1993, Carter et al. 2017). Consequently, changes over space and time in the community composition of macroinvertebrates can indicate degradation in stream habitat quality. Furthermore, macroinvertebrate consumers occupy an intermediate position in stream food webs and are key to ecosystem function because they have both top-down and bottom-up effects on adjacent components of the food web (Wallace and Webster 1996, Nery and Schmera 2016). In the case of grazer-algal interactions, grazing macroinvertebrate abundance is often positively associated with algal growth (Lamberti and Resh 1983, Wallace and Webster 1996), consistent with bottom-up effects. However, the various methods of feeding and patterns of movement of different groups of macroinvertebrates may result in a more complicated relationship with algae in cases where nuisance growth substantially alters the physical environment, as with D. geminata blooms.

The relationships between D. geminata blooms and macroinvertebrate abundances vary among macroinvertebrate groups. For example, Chironomids, a poor-swimming taxon, are often the most abundant family of macroinvertebrates in fresh waters (Cranston 1995) and may seek refuge from flow in D. geminata mats. Larvae of the dorsoventrally flattened family of mayflies, Heptageniidae, adhere closely to rock substrates, move by crawling across stream bottoms, and prefer to graze diatoms on smooth, flat rocks (Peckarsky and Cowan 1995). Therefore, their foraging behavior may be inhibited by dense D. geminata blooms. In contrast, larvae of the highly mobile, swimming mayfly family, Baetidae, may be unaffected by D. geminata blooms because they can climb on the polysaccharide stalks to forage on epiphytic diatoms. These contrasting life history and foraging attributes of 3 abundant families of macroinvertebrates suggest that community composition could be altered by the proliferation of *D. geminata* blooms. Previous studies have demonstrated shifts in macroinvertebrate community composition associated with D. geminata proliferation in streams worldwide (e.g., Kilroy et al. 2009, Gillis and Chalifour 2010, James et al. 2010, Bray et al. 2020). However, the associations between D. geminata proliferations and macroinvertebrate communities have not been formally tested in Colorado Rocky Mountain streams. Documenting those changes in macroinvertebrate communities is important because of the potential for negative effects on other species that interact with higher (trout) and lower (other diatoms) trophic-level taxa in mountain stream food webs.

The purpose of this study was to examine the effects of spatial and temporal variation in D. geminata proliferation on macroinvertebrates in streams around the Rocky Mountain Biological Laboratory (RMBL) in Gunnison County, Colorado, USA, an area where regional trends of earlier spring snow melt and nuisance blooms of D. geminata have been observed (Inouye 2022). We asked: What is the association of spatial and temporal variation in D. geminata with changes in the overall community composition of macroinvertebrates and in the abundance of 3 focal taxa (families): Chironomidae (Diptera), Heptageniidae, and Baetidae (Ephemeroptera)? Considering the natural histories of those 3 families, our specific hypotheses were that increases in D. geminata proliferations over space and time are associated with 1) shifts in overall macroinvertebrate community composition, 2) increases in abundance of midge larvae (Chironomidae), 3) decreases in abundance of some mayfly larvae (Heptageniidae), and 4) no effects on the abundance of other mayfly larvae (Baetidae) because of differences in life-history strategies among Ephemeroptera families.

# METHODS

# Study design

We used both contemporary and historical field-collected datasets to test our hypotheses. Since 1976, BLP and collaborators have documented the community composition of macroinvertebrates in 8 stream sites near RMBL to monitor conditions in streams protected by nonconsumptive water rights—also known as in-stream flow rights—obtained by the RMBL at that time (Buckelew 2021). In 2013, we added surveys of *D. geminata* to the nonconsumptive water rights sampling protocol, following protocols described by James et al. (2015) and West et al. (2020), initiated by C. Kilroy to quantify the presence and proliferation of *D. geminata* in New Zealand streams.

We conducted this study at the 8 sites across an elevation range of ~2800 to 3200 m in 3 streams near RMBL: Copper Creek, East River, and Rustlers Gulch (Fig. 1). All 8 sites are sampled twice during the snow-free season each summer (early during the descending limb of the hydrograph and late during baseflow) to capture species with different seasonal phenologies. Here, we focused our analyses on 9 y of benthic macroinvertebrate samples (2013–2021) collected during baseflow conditions because scouring of the substrate during spring snowmelt results in



Fig. 1. Map of 8 study sites distributed across 3 rivers in Gunnison County, Colorado (and the study's location in the United States; inset): Copper Creek (upstream of Second Crossing, upstream of Judd Falls, upstream of the County Road 317 bridge in the town of Gothic), East River (Oregon Mine Road Crossing, near Avery, near Levi Cabin, and upstream of the County Road 317 bridge south of Gothic), and Rustlers Gulch (upstream of the confluence with the East River). The colors of the symbols indicate relative biovolume of *Didymosphenia geminata* averaged across 9 y (2013–2021), with darker orange symbols having the highest biovolume. We have not observed *D. geminata* blooms at sites indicated with gray symbols (East River Oregon Mine and Rustlers Gulch). Map created using ArcGIS Online (https://arcg.is/0nvLT9).

low *D. geminata* biovolume early in the summer, and proliferation of new mat formation occurs after peak flows decline toward baseflow conditions. We used multivariate analyses to understand how macroinvertebrate community composition varies with *D. geminata* biovolume and linear modeling to assess the relationships between abundance (densities) of the 3 focal taxa and *D. geminata* biovolume.

# Sampling protocols

Over the course of 9 summers (2013–2021), we took 4 samples of macroinvertebrates at all 8 sites using a Hoffman Sampler—a 0.104-m<sup>2</sup> metal box, open on 2 sides, with a fixed stainless-steel mesh upstream opening and a 364-µm-mesh driftnet fastened to the downstream opening. We disturbed the substrate inside the sampler for 1 min, causing resident macroinvertebrates to drift into the net. From 2013 to 2017, we preserved entire samples for identification in the laboratory using expert knowledge (BLP). From 2018 to 2021, we counted and identified all individuals present in the sample in the field and released them back into the stream. We preserved individuals that could not be identified in the field for subsequent identification under a dissecting microscope in the laboratory.

Because effects can vary over spatial scales (e.g., Bray et al. 2016), we estimated the biovolume of D. geminata at 2 scales: microhabitat conditions (sample level: 2020-2021), and macrohabitat conditions (along 3 transects selected to capture representative habitat conditions of each site: 2013-2021). At both scales, we calculated an index of D. geminata biovolume (James et al. 2015, West et al. 2020) as the product of visually estimated % cover and the measured height (mm) of D. geminata inside a glass-bottomed viewing box. At the microhabitat scale, we placed the viewing box inside each Hoffman sampler and estimated D. geminata biovolume before taking the macroinvertebrate samples. For biovolume estimates at the macrohabitat scale, we stretched a meter tape across 3 transects at each site, estimated the D. geminata biovolume inside the viewing box at every ½ m and calculated the mean site biovolume across all measurements/transect, the number of which varied according to the widths of the sites (2013–2021).

# Assessing spatial structure in macroinvertebrate community data

To ensure that our data were not spatially structured, which could influence our analysis results, we checked for spatial autocorrelation in 2 ways. First, we examined spatial autocorrelation in community composition among sites (macrohabitat scale) with a Mantel test (mantel.rtest function from the *ade4* package, version 1.7-22; Dray and Dalfour 2007) in R (version 4.3.1; R Project for Statistical Computing, Vienna, Austria) that correlated a matrix of pairwise Bray–Curtis dissimilarity values between sites with a matrix of pairwise Euclidian distances between sites. Then, we examined spatial autocorrelation in abundances of the 3 focal taxa among sites with Moran's I correlograms (correlog function from the R *pgrimess* package, version 2.0.2; Giraudoux et al. 2023).

# Variation in macroinvertebrate community composition with *D. geminata*

To assess the variation in macroinvertebrate community composition along a gradient of D. geminata biovolume, we used 2 multivariate analyses: permutational multivariate analysis of variance (PERMANOVA; 999 permutations) and nonmetric multidimensional scaling (NMDS). First, we used the adonis2 function in the vegan package (version 2.6-4; Oksanen et al. 2020) in R to test for associations between D. geminata biovolume and macroinvertebrate community composition (using a Bray-Curtis dissimilarity matrix constructed from untransformed macroinvertebrate density data, calculated as the no.  $ind./m^2$  of area sampled). The PERMANOVA also included effects of site and year to account for the potential confounding effects of environmental variation among sites and years on macroinvertebrate community composition. We generated 3 versions of the PERMANOVA model: 1 including the interactions between biovolume  $\times$  year, biovolume  $\times$  site, and biovolume  $\times$ site  $\times$  year; 1 with just the interactions between biovolume  $\times$  year and biovolume  $\times$  site; and 1 with no interaction terms. We applied these analyses to data obtained at both the microhabitat (2020-2021) and macrohabitat (2013-2021) scales, for which we used data from historical surveys of D. geminata biovolume and macroinvertebrate communities. For macroscale analysis we aggregated the 4 macrohabitat samples at each site to obtain 1 value for the density of each taxon at each site. These analyses enabled us to determine if the effects of D. geminata are scale dependent (i.e., whether effects were stronger at smaller or larger scales). We then used NMDS with the metaMDS function in the vegan package, with Bray-Curtis dissimilarity as the distance metric, to display the variation in macroinvertebrate community composition across D. geminata biovolume gradients at both scales. We used the decostand function in the vegan package to relativize the data (method: total). To evaluate stress, we constructed Shepard plots using the stressplot function in the *vegan* package and scree plots using the dimcheckMDS from the goeveg package (version 0.6.5; von Lampe and Schellenberg 2023).

# Relationships of macroinvertebrate abundances with *D. geminata*

To better understand the mechanisms underlying observed shifts in macroinvertebrate community composition, we used generalized linear mixed-effects models (GLMMs; *lme4* package, version 1.1–35.1; Bates et al. 2015) in R to evaluate the relationships between *D. geminata* biovolume and the densities of the 3 focal macroinvertebrate taxa-Chironomidae, Heptageniidae, and Baetidae. We used all 9 y of macroinvertebrate and D. geminata data at the macrohabitat scale and 2 y of data at the microhabitat scale, and we selected either Poisson (appropriate for count data) or negative binomial (appropriate for overdispersed data) error distributions for each model. We tested responses of target taxa to D. geminata biovolume at the family level, which was the finest level of resolution practical for Chironomidae. We constructed each model to examine the responses of specific taxa abundances to increasing D. geminata biovolume (fixed effect) and included random effects of site and year to isolate the D. geminata effect from environmental variation otherwise associated with sites and years. To examine model fit we plotted residuals, and we used Akaike Information Criterion to compare model fit between the 2 error structures, with lower Akaike Information Criterion indicating a more parsimonious model fit. To display the results of the best-fit models for each of the taxa at macrohabitat and microhabitat scales, we constructed partial residual plots that visually isolate the fixed effect of *D. geminata* from the random effects of site and year.

# RESULTS

Over the 9-y study, we collected >93,000 individuals belonging to 37 different families of macroinvertebrates (Table S1). The range of abundance varied over years and sites (Table S2), with the maximum number of individuals (21,154) collected in 2018, and the minimum (5,053) collected in 2017. The maximum total ind./site (7568) were collected at Copper Creek Second Crossing in 2018 and lowest total ind./site (170) at East River Levi in 2014. The 3 focal taxa made up 77% of the total catch. Families Heptageniidae (20%) and Baetidae (12%) are the most abundant families of mayflies in streams near RMBL (percentage of the total benthic fauna at the study sites) and of Rocky Mountain streams in general (Ward and Berner 1980). Chironomidae are typically the most abundant family in streams near RMBL, comprising 45% of the total benthos of the sites during the 9-y study.

The index of didymo biovolume also varied among years and sites, ranging from 0 (Rustlers Gulch and East River Oregon Mine) to 528 (Copper Creek Bridge in 2021). Abundance of macroinvertebrates generally increased at sites, samples, and years where didymo biovolume was high (Tables S3, S4).

# Spatial structure in macroinvertebrate community data

The Mantel test showed a positive relationship between Euclidean distance and Bray–Curtis dissimilarity of invertebrate assemblages (Mantel's r = 0.74, p = 0.002, 999 runs). The Moran's I correlograms showed no evidence for autocorrelation in 2 of the 3 focal taxa (Heptageniidae and Baetidae; Fig. S1A, B). Chironomidae showed evidence of positive spatial autocorrelation at short scales and nega-

tive correlation at long scales (Fig. S1C). Given these results and our knowledge of the system—adjacent sites are either km apart (Fig. 1) or separated by major discontinuities such as pools and tributaries—and that decay in community similarity as a function of distance is ubiquitous (Soininen et al. 2007), we treated the sites as independent.

# Macroinvertebrate community composition varied with *D. geminata*

Macroinvertebrate community composition varied with increasing D. geminata biovolume at both scales. There were no interactions between D. geminata biovolume, year, and site, so we removed the interaction terms from the PERMANOVA models (Table S5). At the microhabitat scale (sample level), PERMANOVA indicated that ~16% of the variation in macroinvertebrate community composition can be explained by *D. geminata* biovolume (partial  $R^2$  = 0.16, pseudo- $F = 24.8_{1.54}$ , permutational-p = 0.001). At this smaller scale there was no effect of site, and year explained 3% of the variation in macroinvertebrate communities. At the macrohabitat scale (site level), the PERMANOVA indicated that ~9% of the variation in macroinvertebrate community composition can be explained by variation in D. geminata biovolume (partial  $R^2 = 0.09$ , pseudo-F =14.3<sub>1,62</sub>, permutational-p = 0.001). At this larger scale, site explained 34% and year explained 4% of the variation in macroinvertebrate communities.

Two-dimensional NMDS ordination plots illustrate that Heptageniidae predominated under low *D. geminata* conditions and Chironomidae predominated under high *D. geminata* conditions at both scales of observation (microhabitat [sample level] goodness of fit: stress = 0.092; macrohabitat [site level] goodness of fit: stress = 0.11; Fig. 2A, B). NMDS plots including the multivariate space of all taxa collected are reported in Fig. S2A, B. Shepard plots of observed dissimilarity vs observed distance showed good fits for both scales (Fig. S3A, B). Scree plots of stress vs dimension showed acceptable stress for all dimensions above 2 at both scales (Fig. S4A, B).

# Relationships between macroinvertebrate densities and *D. geminata*

GLMM results agreed with PERMANOVA and NMDS results, showing a negative relationship between Heptageniidae and *D. geminata* and a positive relationship between Chironomidae and *D. geminata* (Table S6). At the microhabitat scale, the best-fit GLMM model showed decreasing Heptageniidae density as *D. geminata* biovolume increased, with a declining slope coefficient (effect size) of -0.20 (SE = 0.10, z = -2.03, p = 0.04, negative binomial distribution; Fig. 3A). Similarly, at the macrohabitat scale, the best-fit GLMM model showed decreasing Heptageniidae density as *D. geminata* biovolume increased, with a slope coefficient of -0.16 (SE = 0.09, z = -1.80, p = 0.07, negative



Fig. 2. Nonmetric multidimensional scaling (NMDS) ordination of Bray–Curtis dissimilarities in densities  $(no./m^2)$  of 3 focal macroinvertebrate families (Heptageniidae, Chironomidae, Baetidae), constituting 77% of the total benthic invertebrate fauna, sampled at the microhabitat scale (sample-level goodness of fit as stress = 0.092) (A) and the macrohabitat scale (site-level goodness of fit as stress = 0.114) (B). A gradient of *Didymosphenia geminata* biovolume from low to high is represented by grayscale contour lines. See Fig. S2 for NMDS ordination plots representing all taxa and sites.

binomial error distribution; Fig. 3B). In contrast, Baetidae densities did not vary with *D. geminata* biovolume at either scale (microhabitat scale: slope coefficient = 0.13, SE = 0.10, z = 1. 29, p = 0.2, negative binomial distribution; macrohabitat scale: slope coefficient = 0.08, SE = 0.07, z = 1.10; p = 0.3, negative binomial distribution; Fig. 4A, B).

The strongest responses to variation in *D. geminata* biovolume were of Chironomidae. At the microhabitat scale, Chironomidae density increased as *D. geminata* biovolume increased, with a slope coefficient of 0.49 (SE = 0.002, z = 253.13, p < 0.0001, Poisson error distribution [negative binomial distribution did not converge]; Fig. 5A). This



Fig. 3. Partial residual plots of the association between *Didymosphenia geminata* biovolume (standing stock index) and Heptageniidae abundance (density: no./m<sup>2</sup>) at the microhabitat (A) and macrohabitat (B) scales from generalized linear mixed-effects models. Heptageniidae density declined with increasing *D. geminata* biovolume at each scale with slope coefficients (effect sizes) = -0.196 (p = 0.04) and -0.156 (p = 0.07), respectively. Each model included random effects of site and year. Dashed lines represent 95% CI.



Fig. 4. Partial residual plots of the association between *Didymosphenia geminata* biovolume (standing stock index) and Baetidae abundance (density: no./m<sup>2</sup>) at the microhabitat (A) and macrohabitat (B) scales from generalized linear mixed-effects models. Baetidae density was not related to variation in *D. geminata* biovolume. Each model included random effects of site and year.

positive trend was similar at the macrohabitat scale, with a slope coefficient of 0.52 (SE = 0.14, z = 3.66, p = 0.0003, negative binomial distribution; Fig. 5B).

### DISCUSSION

A warming climate is causing declining snow-derived runoff in the western United States (Li et al. 2017), and blooms of *D. geminata* have become a growing concern because of the association between *D. geminata* proliferation and low stream discharge (Kirkwood et al. 2007, 2009). Under those conditions, *D. geminata* proliferations are spreading as nuisance blooms across its native and nonnative ranges (Kilroy et al. 2009, Kumar et al. 2009, Kilroy and Unwin 2011, Richardson et al. 2014). Given this diatom's increasing proliferation, it is important to evaluate



Fig. 5. Partial residual plots of the association between *Didymosphenia geminata* biovolume (standing stock index) and Chironomidae abundance (density: no./m<sup>2</sup>) at the microhabitat (A) and macrohabitat (B) scales from generalized linear mixed-effects models. Chironomidae density increased with increasing *D. geminata* biovolume at each scale with slope coefficients (effect sizes) =  $0.49 \ (p < 0.0001)$  and  $0.52 \ (p = 0.0003)$ , respectively. Each model included random effects of site and year. Dashed lines represent 95% CI.

the impacts of the spread of the nuisance growth form of this species in both its native and invasive ranges (Taylor and Bothwell 2014). We found an overall shift of macroinvertebrate community composition with increasing *D. geminata* biovolume at both microhabitat and macrohabitat scales in native stream systems near RMBL in the western Colorado Rocky Mountains. Moreover, these communitylevel shifts can be attributed to observed ~50% increases in the density of Chironomidae and ~20% decreases in density of Heptageniidae. These shifts in macroinvertebrate family dominance may indicate changes in the quality of stream habitat concurrent with *D. geminata* proliferation and highlight how nuisance blooms of this diatom can alter stream ecosystems and food webs.

# Shifts in macroinvertebrate community composition

Morphological and behavioral attributes of Chironomidae are consistent with the strong positive relationship between its abundance and *D. geminata* biovolume. Chironomidae species have diverse feeding modes but commonly act as collector–gatherers of fine particulate organic matter (Berg 1995), which accumulates within mats of *D. geminata* proliferations (Ladrera et al. 2018). Additionally, Chironomidae are poor swimmers, incapable of controlling movement in the water column, and are very much at the whim of the stream's flow (Pinder 1995). They should, therefore, benefit from the dense stalks of *D. geminata* blooms, which may provide not only a refuge from streamflow, but also an accessible food source. Furthermore, observed shifts in macroinvertebrates to predominantly Chironomidae are indicative of stream habitat degradation (Hilsenhoff 1988).

Likewise, observed reductions in Heptageniidae abundance with increasing *D. geminata* biovolume at both micro- and macrohabitat scales indicate degradation of the stream habitat (Hilsenhoff 1988) and may be linked to their feeding behaviors. Heptageniidae use a variety of mechanisms to feed on benthic algae, but the species present in streams around RMBL require smooth, hard substrates to forage effectively on benthic diatoms (McShaffrey and McCafferty 1988, Peckarsky and Cowan 1995). Foraging movements of Heptageniidae across stream bottoms may be inhibited by *D. geminata* blooms, potentially explaining the observed negative relationship between *D. geminata* blooms and these mayflies, but additional research would be needed to establish that causal link.

The stronger relationship we found between *D. geminata* proliferation and Heptageniidae abundance at the microhabitat than the macrohabitat scale may reflect the heterogeneous distribution of *D. geminata* at the macrohabitat scale. Within sites, certain areas of the stream bottom had dense blooms, whereas other microhabitats had much lower bloom density or lacked noticeable *D. geminata* stalk formation. This pattern likely reflects the integration of habitat heterogeneity at the site level in contrast with the more homogeneous patches of *D. geminata* at the sample scale. This observation of scale dependence is consistent with other studies investigating the frequently positive relationship between environmental heterogeneity and species richness (Stein et al. 2014, Bray et al. 2016). One potential implication of this result is that macroinvertebrate community structure may suffer fewer changes in streams with patchy *D. geminata* proliferations than in streams with fuller and more homogeneous coverage of *D. geminata*. This hypothesis deserves further testing.

In contrast with the other 2 families, we observed no relationship between the density of Baetidae with D. geminata biovolume at either scale, and this lack of relationship may also be related to Baetidae life-history attributes. Baetidae are highly mobile, grazing mayflies that do not need smooth rock surfaces to successfully forage for diatoms (Peckarsky and Cowan 1995, Álvarez and Peckarsky 2005). They are most abundant on rocks with high periphyton abundance (Richards and Minshall 1988), are excellent swimmers, and their mobility improves as they grow (Kutash and Craig 1998). These attributes enable Baetidae to feed on epiphytic diatoms on D. geminata stalks. Therefore, foraging Baetidae are less likely to be inhibited by proliferations or to seek refuge from flow within mats, possibly explaining, in part, why their abundance in the benthos is unaffected by the blooms of *D. geminata*. It is worth noting that the absence of a negative effect of D. geminata proliferation on Baetidae is encouraging because they are considered a foundation species (Ellison et al. 2005)-ubiquitous and strongly interacting with other members of food webs, substantially contributing to ecosystem processes (Álvarez and Peckarsky 2005, 2014).

Similar effects of D. geminata on macroinvertebrate community composition occur worldwide. In New Zealand where this diatom is nonnative and invasive, Chironomidae and Oligochaeta were positively correlated with D. geminata proliferation (Kilroy et al. 2009, Jellyman and Harding 2016, Anderson et al. 2020). Abundance of the common mayfly Deleatidium (Leptophebiidae) concurrently decreased in streams with D. geminata blooms (Anderson et al. 2020). In streams of northern Spain, D. geminata proliferation was associated with declines in Heptageniidae and increases in Chironomidae and Oligochaeta (Ladrera et al. 2018), as well as a decline in overall macroinvertebrate diversity (Shannon index; Sanmiguel et al. 2016, Ladrera et al. 2018). In Québec, Canada, Ephemeroptera, Plecoptera, and Trichoptera declined with increasing proliferation of D. geminata (Gillis and Chalifour 2010), and in the Catskills in New York, USA, D. geminata was negatively correlated with macroinvertebrate richness (Richardson et al. 2014). In a South Dakota, USA, stream, lower abundance of Ephemeroptera, Plecoptera, and Trichoptera larvae were observed in areas with D. geminata (James et al. 2010). Therefore, we suspect that the consistently observed shifts in macroinvertebrate community composition may have similar trophic effects on other components of stream food webs as *D. geminata* blooms increase across its native and invasive ranges.

Because macroinvertebrates are an important link in food chains, trophic effects of D. geminata proliferation on macroinvertebrate communities may have consequences for predatory vertebrates. For example, Rainbow Trout (Oncorhynchus mykiss [Walbaum, 1792]) growth was inversely related to winter D. geminata coverage for smaller, though not larger, individuals in Montana, USA (Dunnigan and Terazzas 2021), and there was a 90% decline in insectivorous fish biomass with increasing D. geminata biovolume found in New Zealand streams (Jellyman and Harding 2016). This effect has also been observed in Rocky Mountain systems, where streams with proliferations of D. geminata were associated with reduced growth rate of Brook Trout (Salvelinus fontinalis [Mitchill, 1814]) compared with similar streams with no D. geminata proliferations (B. W. Taylor, North Carolina State University, Raleigh, North Carolina, USA, personal communication). Our data suggest that this negative effect of D. geminata proliferation on the top consumers of macroinvertebrates may be explained by the predominance of small-bodied macroinvertebrate prey (chironomids) in streams with D. geminata blooms compared with streams where blooms are absent, in which mayflies, a higher quality food source (Allan 1981), are more abundant. However, other studies have reported little to no effect of D. geminata on stream-dwelling salmonid populations (James and Chipps 2016, Clancy et al. 2021). A full study of fish energetics coupled with estimates of available prey biomass is necessary to demonstrate definitively that D. geminata proliferation negatively affects fish growth.

Didymosphenia geminata proliferation not only has the potential to affect higher trophic levels, but also has been shown to affect other species of diatoms (Bray et al. 2020). Resistance of native periphyton communities to D. geminata invasions may relate to successional stage (Floder and Kilroy 2009), but results of previous studies indicate that the type and extent of this effect are not totally clear. For example, Gillis and Lavoie (2014) suggested that the presence of D. geminata blooms is associated with changes in algal community structure and diversity; however, they observed little effect of increasing D. geminata biovolume on other diatoms. Sanmiguel et al. (2016), on the other hand, observed higher richness and diversity in benthic algae communities with increasing *D. geminata* biovolume, and Ladrera et al. (2018) found that D. geminata presence was associated with increased abundance of small diatoms in northern Spain.

## D. geminata—An ecosystem engineer

Given the extensive alterations in stream habitat and consequent trophic effects on many components of stream ecosystems, we contend that *D. geminata* can be considered an ecosystem engineer (Bray 2014, Ladrera et al. 2018, Bray et al. 2020, Clancy et al. 2021). Ecosystem engineers influ-

ence the acquisition of resources of other species by physically altering their environment. In this case, D. geminata physically changes the substrate available for macroinvertebrates-from smooth rocks with a thin layer of diatoms to thick mats of entangled polysaccharide stalks and associated epiphytes and accumulated detritus-which may both positively and negatively affect the ability of macroinvertebrates to forage, depending on feeding mode. Furthermore, D. geminata proliferations have been shown to alter the hydrology in the benthic environment. Larned et al. (2011) experimentally examined the effects of D. geminata on nearbed flow, observing increased flows at the mat surfaces (enhancing nutrient delivery to D. geminata cells) and decreased flows within mats (enhancing nutrient retention). More specifically, D. geminata decreases wake turbulence and form-induced stresses within its mats and increases turbulent and total shear stress above its mats (Larned et al. 2011). Such habitat engineering by D. geminata is not only favorable for its own nutrient acquisition but also has the potential to affect stream macroinvertebrate communities.

Several studies have shown that alterations in near-bed flows change microhabitats and thereby have effects on macroinvertebrate communities (Lancaster and Hildrew 1993, Growns and Davis 1994, Hart et al. 1996, Hart and Finelli 1999). Our observation that Chironomidae abundance increased with D. geminata proliferation is consistent with these flow modifications. As flow increases, Chironomidae are vulnerable to being eroded out of the substrate (Wiley 1981), and, consequently, D. geminata mats could provide a flow refuge. In contrast, Heptageniidae are not favored in low-flow conditions (Peckarsky and Cowan 1995). Instead, they are morphologically adapted to cling to hard substrates with high near-bed flows (Statzner and Holm 1982), potentially contributing to their observed declining abundance with increasing D. geminata biovolume. Baetidae, which were not affected by D. geminata proliferation, are well adapted to forage on epiphytes growing on D. geminata stalks in areas of higher flow and often select high-flow habitats (Peckarsky and Cowan 1995).

In addition to affecting stream flow, *D. geminata* has been shown to alter benthic  $O_2$  levels, with increased  $O_2$ levels above mats (caused by turbulence) and depleted levels within them (caused by reduced flows) (Larned et al. 2011). Chironomidae can tolerate the reduced  $O_2$  levels characteristic within *D. geminata* mats (Cranston 1995, Connolly et al. 2004), whereas mayflies show comparatively high sensitivity to low  $O_2$  conditions (Connolly et al. 2004) and demonstrate behavioral  $O_2$  regulation by moving out of microhabitats with low  $O_2$  levels (Wiley and Kohler 1980).

### Study limitations

This study was observational, based on long-term survey data. Therefore, the data do not elucidate cause and effect between the variables. Well-designed experiments manipulating didymo biovolume that test the consequences on macroinvertebrate communities would enable definitive conclusions that variation in didymo is the cause of observed community shifts. In addition, taxonomic resolution at the family level was most practical for this study, and although behavioral attributes of the 3 focal taxa hypothesized to contribute to their responses to variation in didymo biovolume are relatively consistent at the family level, future research at finer taxonomic resolution would be valuable. Also, while 9 y of data were available to analyze effects of didymo on macroinvertebrates at the macrohabitat (site) scale, conclusions at the microhabitat (sample) scale would be strengthened by more years of observations of relationships between didymo biovolume and macroinvertebrate communities. Finally, when enough data become available, a meta-analysis of effects of didymo on macroinvertebrate communities at a larger geographic scale would reinforce conclusions drawn from this study, which is focused on a single watershed.

### **Broader implications**

Although processes such as habitat transformation or ecosystem engineering (Falk-Petersen et al. 2006) may facilitate *D. geminata* invasions, a key contribution of this study to the literature on D. geminata is the observation that nuisance proliferations occur in its native range, with ecological consequences. Qualitatively, D. geminata appears to have similar effects on macroinvertebrate community composition across its native and nonnative (including invasive) distributions, with increases in chironomids and decreases in some mayflies (Kilroy et al. 2009, Gillis and Chalifour 2010, Jellyman and Harding 2016, Ladrera et al. 2018). Taylor and Bothwell (2014) note that establishing whether a nuisance organism is native or invasive presents important information for management, i.e., whether the focus should be on limiting dispersal or managing environmental conditions. Therefore, informed management decisions require knowledge of the consequences of increasing D. geminata proliferation whether native or invasive.

Because climate change is increasing the frequency of extreme weather events—importantly, increasing the variability of winter precipitation—streamflow will continue to vary among years. Furthermore, the directional trend toward warming and drying in mountainous regions is expected to result in earlier spring snowmelt and more frequent occurrences of extremely low summer streamflow. These conditions favor proliferations of *D. geminata* within its native range in the mountain western USA. Under conditions of accelerating climate change, it is increasingly important to understand the impacts of nuisance blooms of this ecosystem engineer on macroinvertebrate community composition and the potential for trophic effects to alter stream food webs.

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Data availability statement: Data are archived and available by contacting the Science Director at Rocky Mountain Biological Laboratory (sd@rmbl.org), and all R code used in analysis is available in Appendix S1.

# LITERATURE CITED

- Aiken, E. K., and S. A. Rauscher. 2020. Evaluation of the climate extremes index over the United States using 20th and mid-21st century North American regional climate change assessment program data. International Journal of Climatology 40: 1542–1560.
- Allan, J. D. 1981. Determinants of diet of Brook Trout (*Salvelinus fontinalis*) in a mountain stream. Canadian Journal of Fisheries and Aquatic Sciences 38:184–192.
- Álvarez, M., and B. L. Peckarsky. 2005. How do grazers affect periphyton heterogeneity in streams? Oecologia 142:576–587.
- Álvarez, M., and B. L. Peckarsky. 2014. Cascading effects of predatory fish on the composition of benthic algae in high-altitude streams. Oikos 123:120–128.
- Anderson, I. J., M. K. Saiki, K. Sellheim, and J. E. Merz. 2014. Differences in benthic macroinvertebrate assemblages associated with a bloom of *Didymosphenia geminata* in the Lower American River, California. Southwestern Naturalist 59:389–395.
- Anderson, S. E., G. P. Closs, and C. D. Matthaei. 2020. Agricultural land-use legacy, the invasive alga *Didymosphenia geminata* and invertebrate communities in upland streams with natural flow regimes. Environmental Management 65:804–817.
- Balik, J. A., D. C. West, and B. W. Taylor. 2021. High-discharge disturbance does not alter the seasonal trajectory of nutrient uptake in a montane stream. Hydrobiologia 848:4535–4550.
- Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using *lme4*. Journal of Statistical Software 67.
- Berg, M. B. 1995. Larval food and feeding behaviour. Pages 136– 168 in P. D. Armitage, P. S. Cranston, and L. C. V. Pinder (editors). The Chironomidae: Biology and ecology of non-biting midges. Springer, Berlin, Germany.
- Bergey, E. A., and S. A. Spaulding. 2015. *Didymosphenia*: It's more complicated. BioScience 65:225.
- Bishop, I. W., and S. A. Spaulding. 2017. Life cycle size dynamics in *Didymosphenia geminata* (Bacillariophyceae). Journal of Phycology 53:652–663.

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- Bothwell, M. L., B. W. Taylor, and C. Kilroy. 2014. The didymo story: The role of low dissolved phosphorus in the formation of *Didymosphenia geminata* blooms. Diatom Research 29:229– 236.
- Brahney, J., M. L. Bothwell, L. Capito, C. A. Gray, S. E. Null, B. Menounos, and P. J. Curtis. 2021. Glacier recession alters stream water quality characteristics facilitating bloom formation in the benthic diatom *Didymosphenia geminata*. Science of the Total Environment 764:142856.
- Bray, J., J. S. Harding, C. Kilroy, P. Broady, and P. Gerbeaux. 2016. Physicochemical predictors of the invasive diatom *Didymosphenia geminata* at multiple spatial scales in New Zealand rivers. Aquatic Ecology 50:1–14.
- Bray, J. P. 2014. The invasion ecology of *Didymosphenia geminata*. PhD Dissertation. University of Canterbury, Christchurch, New Zealand.
- Bray, J. P., C. Kilroy, P. Gerbeaux, F. J. Burdon, and J. S. Harding. 2020. Ecological processes mediate the effects of the invasive bloom-forming diatom *Didymosphenia geminata* on stream algal and invertebrate assemblages. Hydrobiologia 847:177–190.
- Buckelew, M. C. 2021. Expanding in-stream flow rights as a mechanism for water conservation and aquatic ecosystem preservation. Yale School of the Environment, New Haven, Connecticut. (Available from: https://highplainsstewardship.org/non-con sumptive-water-rights-as-a-landscape-conservation-tool/)
- Cairns, J., and J. R. Pratt. 1993. A history of biological monitoring using benthic macroinvertebrates. Pages 10–27 *in* D. M. Rosenberg and V. H. Resh (editors). Freshwater biomonitoring and benthic macroinvertebrates. Chapman & Hall, New York, New York.
- Carter, J. L., V. H. Resh, and M. J. Hannaford. 2017. Macroinvertebrates as biotic indicators of environmental quality. Pages 293–318 in G. A. Lamberti and F. R. Hauer (editors). Methods in stream ecology. 3<sup>rd</sup> edition. Academic Press, San Diego, California.
- Clancy, N. G., J. Brahney, J. Dunnigan, and P. Budy. 2021. Effects of a diatom ecosystem engineer (*Didymosphenia geminata*) on stream food webs: Implications for native fishes. Canadian Journal of Fisheries and Aquatic Sciences 78:154–164.
- Connolly, N. M., M. R. Crossland, and R. G. Pearson. 2004. Effect of low dissolved oxygen on survival, emergence, and drift of tropical stream macroinvertebrates. Journal of the North American Benthological Society 23:251–270.
- Cranston, P. S. 1995. Introduction. Pages 1–7 *in* P. D. Armitage, P. S. Cranston, and L. C. V. Pinder (editors). The Chironomidae: Biology and ecology of non-biting midges. Springer, Berlin, Germany.
- Cullis, J. D. S., D. M. McKnight, and S. A. Spaulding. 2015. Hydrodynamic control of benthic mats of *Didymosphenia geminata* at the reach scale. Canadian Journal of Fisheries and Aquatic Sciences 72:902–914.
- Dray, S., and A.-B. Dufour. 2007. The *ade4* package: Implementing the duality diagram for ecologists. Journal of Statistical Software 22:1–20.
- Dunnigan, J. L., and M. M. Terrazas. 2021. Factors influencing Rainbow Trout annual growth in a large, regulated river. Transactions of the American Fisheries Society 150:89–114.
- Ellison, A. M., M. S. Bank, B. D. Clinton, E. A. Colburn, K. Elliott, C. R. Ford, D. R. Foster, B. D. Kloeppel, J. D. Knoepp, G. M.

Lovett, J. Mohan, D. A. Orwig, N. L. Rodenhouse, W. V. Sobczak, K. A. Stinson, J. K. Stone, C. M. Swan, J. Thompson, B. Von Holle, and J. R. Webster. 2005. Loss of foundation species: Consequences for the structure and dynamics of forested ecosystems. Frontiers in Ecology and the Environment 3:479–486.

- Falk-Petersen, J., T. Bøhn, and O. Sandlund. 2006. On the numerous concepts of invasion biology. Biological Invasions 8:1409–1424.
- Floder, S., and C. Kilroy. 2009. *Didymosphenia geminata* (Protista, Bacillariophyceae) invasion, resistance of native periphyton communities and implications for dispersal and management. Biodiversity and Conservation 18:3808–3824.
- Fyfe, J. C., C. Derksen, L. Mudryk, G. M. Flato, B. D. Santer, N. C. Swart, N. P. Molotch, X. Zhang, H. Wan, V. K. Arora, J. Scinocca, and Y. Jiao. 2017. Large near-term projected snowpack loss over the western United States. Nature Communications 8:14996.
- Gil-Alana, L. A. 2021. Time trends and persistence in the snow-pack percentages by watershed in Colorado. Pages 81–90 *in* M. Saifullah (editor). Weather forecasting. IntechOpen, London, United Kingdom.
- Gillis, C.-A., and M. Chalifour. 2010. Changes in the macrobenthic community structure following the introduction of the invasive algae *Didymosphenia geminata* in the Matapedia River (Québec, Canada). Hydrobiologia 647:63–70.
- Gillis, C.-A., and I. Lavoie. 2014. A preliminary assessment of the effects of *Didymosphenia geminata* nuisance growths on the structure and diversity of diatom assemblages of the Restigouche River basin, Quebec, Canada. Diatom Research 29:281–292.
- Giraudoux, P., J.-P. Antonietti, C. Beale, U. Groemping, R. Lancelot, D. Pleydell, and M. Treglia. 2023. *pgirmess*: Spatial analysis and data mining for field ecologists. (Available from: https:// cran.r-project.org/web/packages/pgirmess/index.html)
- Gómez-Gener, L., A. Lupon, H. Laudon, and R. A. Sponseller. 2020. Drought alters the biogeochemistry of boreal stream networks. Nature Communications 11:1795.
- Growns, I. O., and J. A. Davis. 1994. Longitudinal changes in nearbed flows and macroinvertebrate communities in a Western Australian stream. Journal of the North American Benthological Society 13:417–438.
- Hart, D. D., B. D. Clark, and A. Jasentuliyana. 1996. Fine-scale field measurement of benthic flow environments inhabited by stream invertebrates. Limnology and Oceanography 41:297–308.
- Hart, D. D., and C. M. Finelli. 1999. Physical-biological coupling in streams: The pervasive effects of flow on benthic organisms. Annual Review of Ecology and Systematics 30:363–395.
- Hidalgo, H. G., T. Das, M. D. Dettinger, D. R. Cayan, D. W. Pierce, T. P. Barnett, G. Bala, A. Mirin, A. W. Wood, C. Bonfils, B. D. Santer, and T. Nozawa. 2009. Detection and attribution of streamflow timing changes to climate change in the western United States. Journal of Climate 22:3838–3855.
- Hilsenhoff, W. L. 1988. Rapid field assessment of organic pollution with a family-level biotic index. Journal of the North American Benthological Society 7:65–68.
- Inouye, D. W. 2022. Climate change and phenology. WIREs Climate Change 13:e764.
- IPCC, H.-O. Pörtner, D. C. Roberts, M. M. B. Tignor, E. Poloczanska, K. Mintenbeck, A. Alegría, M. Craig, S. Langsdorf, S.Löschke, V. Möller, A. Okem, and B. Rama. 2022. Climate change

2022 – Impacts, adaptation and vulnerability: Working Group II contribution to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. 1<sup>st</sup> edition. Cambridge University Press, New York, New York.

- James, D. A., M. L. Bothwell, S. R. Chipps, and J. Carreiro. 2015. Use of phosphorus to reduce blooms of the benthic diatom *Didymosphenia geminata* in an oligotrophic stream. Freshwater Science 34:1272–1281.
- James, D. A., and S. R. Chipps. 2016. Influence of *Didymosphenia geminata* on prey composition and associated diet and growth of Brown Trout. Transactions of the American Fisheries Society 145:195–205.
- James, D. A., S. H. Ranney, S. R. Chipps, and B. D. Spindler. 2010. Invertebrate composition and abundance associated with *Didy-mosphenia geminata* in a montane stream. Journal of Freshwater Ecology 25:235–241.
- Jellyman, P. G., and J. S. Harding. 2016. Disentangling the stream community impacts of *Didymosphenia geminata*: How are higher trophic levels affected? Biological Invasions 18:3419–3435.
- Kilroy, C., and M. L. Bothwell. 2012. *Didymosphenia geminata* growth rates and bloom formation in relation to ambient dissolved phosphorus concentration. Freshwater Biology 57:641–653.
- Kilroy, C., S. T. Larned, and B. J. F. Biggs. 2009. The non-indigenous diatom *Didymosphenia geminata* alters benthic communities in New Zealand rivers. Freshwater Biology 54:1990–2002.
- Kilroy, C., and M. Unwin. 2011. The arrival and spread of the bloom-forming, freshwater diatom, *Didymosphenia geminata*, in New Zealand. Aquatic Invasions 6:249–262.
- Kirkwood, A. E., L. J. Jackson, and E. McCauley. 2009. Are dams hotspots for *Didymosphenia geminata* blooms? Freshwater Biology 54:1856–1863.
- Kirkwood, A. E., T. Shea, L. J. Jackson, and E. McCauley. 2007. *Didymosphenia geminata* in two Alberta headwater rivers: An emerging invasive species that challenges conventional views on algal bloom development. Canadian Journal of Fisheries and Aquatic Sciences 64:1703–1709.
- Kumar, S., S. A. Spaulding, T. J. Stohlgren, K. A. Hermann, T. S. Schmidt, and L. L. Bahls. 2009. Potential habitat distribution for the freshwater diatom *Didymosphenia geminata* in the continental US. Frontiers in Ecology and the Environment 7:415–420.
- Kutash, T. N., and D. A. Craig. 1998. Ontogenetic effects on locomotory gaits in nymphs of *Baetis tricaudatus* Dodds (Ephemeroptera:Baetidae). Journal of the North American Benthological Society 17:475–488.
- Ladrera, R., J. Gomà, and N. Prat. 2018. Effects of *Didymosphenia geminata* massive growth on stream communities: Smaller organisms and simplified food web structure. PLOS One 13:e0193545.
- Lamberti, G. A., and V. H. Resh. 1983. Stream periphyton and insect herbivores: An experimental study of grazing by a caddisfly population. Ecology 64:1124–1135.
- Lancaster, J., and A. G. Hildrew. 1993. Flow refugia and the microdistribution of lotic macroinvertebrates. Journal of the North American Benthological Society 12:385–393.
- Larned, S. T., and C. Kilroy. 2014. Effects of *Didymosphenia* geminata removal on river macroinvertebrate communities. Journal of Freshwater Ecology 29:345–362.

- Larned, S. T., A. I. Packman, D. R. Plew, and K. Vopel. 2011. Interactions between the mat-forming alga *Didymosphenia geminata* and its hydrodynamic environment. Limnology and Oceanography: Fluids and Environments 1:4–22.
- Li, D., M. L. Wrzesien, M. Durand, J. Adam, and D. P. Lettenmaier. 2017. How much runoff originates as snow in the western United States, and how will that change in the future? Geophysical Research Letters 44:6163–6172.
- Lute, A. C., and J. T. Abatzoglou. 2014. Role of extreme snowfall events in interannual variability of snowfall accumulation in the western United States. Water Resources Research 50:2874–2888.
- Marshall, B. D. 2007. Effects of Libby Dam, habitat, and an invasive diatom, *Didymosphenia geminata*, on benthic macroinvertebrate assemblages of the Kootenai River, Montana. Prepared for the Montana Department of Fish Wildlife and Parks, Kalispell Montana.
- Marx, A., R. Kumar, S. Thober, O. Rakovec, N. Wanders, M. Zink, E. F. Wood, M. Pan, J. Sheffield, and L. Samaniego. 2018. Climate change alters low flows in Europe under global warming of 1.5, 2, and 3 °C. Hydrology and Earth System Sciences 22:1017–1032.
- McShaffrey, D., and W. P. McCafferty. 1988. Feeding behavior of *Rhithrogena pellucida* (Ephemeroptera:Heptageniidae). Journal of the North American Benthological Society 7:87–99.
- Milly, P. C. D., and K. A. Dunne. 2020. Colorado River flow dwindles as warming-driven loss of reflective snow energizes evaporation. Science 367:1252–1255.
- Moslemi, J. 2010. Influences of environmental change on nutrient cycling in temperate and tropical streams. PhD Dissertation. Cornell University, Ithaca, New York.
- Nery, T., and D. Schmera. 2016. The effects of top-down and bottomup controls on macroinvertebrate assemblages in headwater streams. Hydrobiologia 763:173–181.
- Oksanen, J., G. L. Simpson, F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O'Hara, P. Solymos, M. H. H. Stevens, E. Szoecs, H. Wagner, M. Barbour, M. Bedward, B. Bolker, D. Borcard, G. Carvalho, M. Chirico, M. De Caceres, S. Durand, H. B. A. Evangelista, R. FitzJohn, M. Friendly, B. Furneaux, G. Hannigan, M. O. Hill, L. Lahti, D. McGlinn, M.-H. Ouellette, E. R. Cunha, T. Smith, A. Stier, C. J. F. Ter Braak, and J. Weedon. 2020. *vegan*: Community ecology package. (Available from: https://cran.r -project.org/web/packages/vegan/index.html)
- Peckarsky, B. L., and C. A. Cowan. 1995. Microhabitat and activity periodicity of predatory stoneflies and their mayfly prey in a western Colorado stream. Oikos 74:513–521.
- Pinder, L. C. V. 1995. Biology of the eggs and first-instar larvae. Pages 87–106 in P. D. Armitage, P. S. Cranston, and L. C. V. Pinder (editors). The Chironomidae: Biology and ecology of non-biting midges. Springer, Berlin, Germany.
- Richards, C., and G. W. Minshall. 1988. The Influence of periphyton abundance on *Baetis bicaudatus* distribution and colonization in a small stream. Journal of the North American Benthological Society 7:77–86.
- Richardson, D. C., I. A. Oleksy, T. J. Hoellein, D. B. Arscott, C. A. Gibson, and S. M. Root. 2014. Habitat characteristics, temporal variability, and macroinvertebrate communities associated with a mat-forming nuisance diatom (*Didymosphenia geminata*) in Catskill mountain streams, New York. Aquatic Sciences 76:553–564.

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- Rixen, C., T. T. Høye, P. Macek, R. Aerts, J. M. Alatalo, J. T. Anderson, P. A. Arnold, I. C. Barrio, J. W. Bierke, M. P. Björkman, D. Blok, G. Blume-Werry, J. Boike, S. Bokhorst, M. Carbognani, C. T. Christiansen, P. Convey, E. J. Cooper, J. H. C. Cornelissen, S. J. Coulson, E. Dorrepaal, B. Elberling, S. C. Elmendorf, C. Elphinstone, T. G. W. Forte, E. R. Frei, S. R. Geange, F. Gehrmann, C. Gibson, P. Grogan, A. H. Halbritter, J. Harte, G. H. R. Henry, D. W. Inouye, R. E. Irwin, G. Jespersen, I. S. Jónsdóttir, J. Y. Jung, D. H. Klinges, G. Kudo, J. Lämsä, H. Lee, J. J. Lembrechts, S. Lett, J. S. Lynn, H. M. R. Mann, M. Mastepanov, J. Morse, I. H. Myers-Smith, J. Olofsson, R. Paavola, A. Petraglia, G. K. Phoenix, P. Semenchuk, M. B. Siewert, R. Slatyer, M. J. Spasojevic, K. Suding, P. Sullivan, K. L. Thompson, M. Väisänen, V. Vandvik, S. Venn, J. Walz, R. Way, J. M. Welker, S. Wipf, and S. Zong. 2022. Winters are changing: Snow effects on Arctic and alpine tundra ecosystems. Arctic Science 8:572-608.
- Robinson, C. T., and G. W. Minshall. 1986. Effects of disturbance frequency on stream benthic community structure in relation to canopy cover and season. Journal of the North American Benthological Society 5:237–248.
- Rogers, J. B., E. D. Stein, M. W. Beck, and R. F. Ambrose. 2020. The impact of climate change induced alterations of streamflow and stream temperature on the distribution of riparian species. PLOS One 15:e0242682.
- Sanmiguel, A., S. Blanco, I. Álvarez-Blanco, C. Cejudo-Figueiras, A. Escudero, M. E. Pérez, G. Noyón, and E. Bécares. 2016. Recovery of the algae and macroinvertebrate benthic community after *Didymosphenia geminata* mass growths in Spanish rivers. Biological Invasions 18:1467–1484.
- Soininen, J., R. McDonald, and H. Hillebrand. 2007. The distance decay of similarity in ecological communities. Ecography 30:3–12.
- Solander, K. C., K. E. Bennett, and R. S. Middleton. 2017. Shifts in historical streamflow extremes in the Colorado River Basin. Journal of Hydrology: Regional Studies 12:363–377.
- Spaulding, S. A., and E. Elwell. 2007. Increase in nuisance blooms and geographic expansion of the freshwater diatom *Didymosphenia geminata*. Open-File Report 2007–1425. United States Geological Survey, Reston, Virginia. (Available from: http:// pubs.er.usgs.gov/publication/ofr20071425)
- Spaulding, S. A., J. R. Stone, S. A. Norton, A. Nurse, and J. E. Saros. 2020. Paleoenvironmental context for the Late Pleistocene

appearance of *Didymosphenia* in a North American alpine lake. Aquatic Sciences 82:10.

- Statzner, B., and T. F. Holm. 1982. Morphological adaptations of benthic invertebrates to stream flow: An old question studied by means of a new technique (Laser Doppler Anemometry). Oecologia 53:290–292.
- Stein, A., K. Gerstner, and H. Kreft. 2014. Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. Ecology Letters 17:866–880.
- Taylor, B. W., and M. L. Bothwell. 2014. The origin of invasive microorganisms matters for science, policy, and management: The case of *Didymosphenia geminata*. BioScience 64:531–538.
- Taylor, B. W., and M. L. Bothwell. 2015. Response to Bergey and Spaulding. BioScience 65:226.
- USEPA (United States Environmental Protection Agency). 2016. What climate change means for Colorado. (Available from: https://19january2017snapshot.epa.gov/sites/production/files /2016-09/documents/climate-change-co.pdf)
- von Lampe, F., and J. Schellenberg. 2023. goeveg: Functions for community data and ordinations. (Available from: https:// cran.r-project.org/web/packages/goeveg/index.html)
- Wallace, J. B., and J. R. Webster. 1996. The role of macroinvertebrates in stream ecosystem function. Annual Review of Entomology 41:115–139.
- Ward, J. V., and L. Berner. 1980. Abundance and altitudinal distribution of Ephemeroptera in a Rocky Mountain stream. Pages 169–177 in J. F. Flannagan and K. E. Marshall (editors). Advances in Ephemeroptera biology. Plenum Press, New York, New York.
- West, D. C., J. A. Balik, M. Owens, and B. W. Taylor. 2020. *Didymosphenia geminata* blooms are not exclusively driven by low phosphorus under experimental conditions. Hydrobiologia 847:1057–1069.
- Wiley, M. J. 1981. An analysis of some factors influencing the successful penetration of sediment by chironomid larvae. Oikos 36:296–302.
- Wiley, M. J., and S. L. Kohler. 1980. Positioning changes of mayfly nymphs due to behavioral regulation of oxygen consumption. Canadian Journal of Zoology 58:618–622.
- Xiao, M., B. Udall, and D. P. Lettenmaier. 2018. On the causes of declining Colorado River streamflows. Water Resources Research 54:6739–6756.