Aquat Sci (2014) 76:553–564
DOI 10.1007/s00027-014-0354-7

Aquatic Sciences

RESEARCH ARTICLE

Habitat characteristics, temporal variability, and macroinvertebrate communities associated with a mat-forming nuisance diatom (*Didymosphenia geminata*) in Catskill mountain streams, New York

David C. Richardson · Isabella A. Oleksy · Timothy J. Hoellein · David B. Arscott · Catherine A. Gibson · Samantha M. Root

Received: 14 February 2014 / Accepted: 26 May 2014 / Published online: 20 July 2014

Abstract *Didymosphenia geminata* has recently and rapidly greatly expanded its range and abundance, sometimes as an exotic invasive and other times as a nuisance ('native invader') within its hypothesized native range, including the northeastern United States. *D. geminata* mats are visually conspicuous and can grow >10 cm thick. Mats first appeared in the eastern Catskill mountains (New York) in 2009. Our objectives were to (1) document *D. geminata* growth in three impounded or regulated rivers in the eastern Catskill mountains from 2010 to 2012 and (2) measure the effects of *D. geminata* mats on macroinvertebrates. The highest *D. geminata* cell densities were downstream of reservoir outflows in two of three streams. *D. geminata* mat development peaked in the summer each year, but maximum coverage and cell density was variable among years. *D. geminata* cover was negatively correlated with 10 days maximum antecedent shear stress, and the year with lowest mean *D. geminata* cover had multiple tropical storms and floods, suggesting that low variation in flow allows for *D. geminata* mat proliferation. Across sites, *D. geminata* density was negatively correlated with nitrate concentrations. *D. geminata* density was negatively related to macroinvertebrate richness suggesting that *D. geminata* mats may negatively affect aquatic food webs. *D. geminata* appears to be a nuisance species with similar habitat characteristics and growth where it is both a native invader and an invasive species.

Keywords *Didymosphenia geminata* · Didymo · Native invaders · Nuisance diatom

D. C. Richardson (✉) · I. A. Oleksy
SUNY New Paltz, 1 Hawk Drive, New Paltz, NY 12561, USA
e-mail: richardsond@newpaltz.edu

I. A. Oleksy
University of New Hampshire, 56 College Road, Durham, NH 03824, USA

T. J. Hoellein
Loyola University Chicago, 1032 W. Sheridan Road, Chicago, IL 60660, USA

D. B. Arscott
Stroud Water Research Center, 970 Spencer Road, Avondale, PA 19311, USA

C. A. Gibson
Skidmore College, 815 North Broadway, Saratoga Springs, NY 12866, USA

S. M. Root
Bard College, 30 Campus Road, Annandale-on-Hudson, NY 12504, USA

Introduction

Biological invasions are a major threat to freshwater environments and the ecosystem services they provide (Ehrenfeld 2010; Strayer 2010, 2012). Invasive species are conventionally thought of as non-native organisms (i.e., alien or foreign), but recently the term 'native invaders' has been defined. Native species may become invasive in their native range when new niches open through modifications to their environment or when other native species are removed (Simberloff 2011). These native populations may then increase to nuisance levels and dominate communities (Carey et al. 2012). Native species may also initiate invasive population dynamics when human activities facilitate their movement to previously unoccupied locations within the boundaries of their native range (Drake and Mandrak 2010; Kilroy and Unwin 2011). Invasions by native species may be deleterious for other species or ecosystem function

because even small or temporary shifts in relative abundances of species can have cascading effects on food webs and ecosystem processes (Pace et al. 1999; Carey et al. 2012).

Studies of invasive species in freshwaters are biased towards vertebrates, mollusks, and large vascular plants; while, in general, smaller aquatic organisms are less often studied, in part because of inconclusive documentation of their historic range (Strayer 2010; Carey et al. 2012). For example, the historic range of the freshwater diatom, *Didymosphenia geminata* is not well established (Flöder and Kilroy 2009). *D. geminata* is a large diatom species (~100 µm long) that produces sulfated polysaccharide stalks and forms nuisance mats that can grow >10 cm thick with 100 % cover of streambeds. *D. geminata* is thought to be native to oligotrophic streams and rivers in boreal and high elevation sites throughout the Northern Hemisphere (Pite et al. 2009; Kumar et al. 2009). In recent records (<100 years), *D. geminata* has been documented as a rare taxon in North America (e.g., Cleve 1965; Patrick and Reimer 1975; Lavery et al. 2014). However, within the past 20 years, *D. geminata* has appeared as a dominant member of periphyton communities within and outside its hypothesized native range globally (e.g., Blanco and Ector 2009; Kilroy and Unwin 2011; Reid et al. 2012). Documentation of *D. geminata* range expansion and mat occurrence in the western and central US has been ongoing for the last 10–15 years (Spaulding and Elwell 2007), but nuisance *D. geminata* mats were first documented in the northeastern US and eastern Canada more recently (Lavery et al. 2014). *D. geminata* range expansion appears to be rapid, but there has been limited assessment of *D. geminata* growth or the physiochemical conditions triggering *D. geminata* stalk production (Kirkwood et al. 2007; Bergey et al. 2010).

Most algae with luxurious or nuisance periphyton accumulations reproduce rapidly in eutrophic waters, but thick mats of *D. geminata* have been mostly documented in oligotrophic environments. Recent evidence suggests *D. geminata*'s thick mats facilitate its growth and nutrient uptake in oligotrophic streams. Mats may reduce bedform-induced stresses and near-bed turbulent velocity, which protects cells from scour, but also may increase turbulent shear stress just above the mat which facilitates dissolved and particulate phosphorus (P) exchange (Larned et al. 2011; Aboal et al. 2012). In addition, the three-dimensional mat structure may create redox gradients where microbial activity may facilitate the dissociation of iron (Fe)-bound P (Sundareshwar et al. 2011). Finally, the stalks have been shown to host increased enzyme activity and organic P hydrolysis which may enable P transport directly to the cells (Ellwood and Whitton 2007; Aboal et al. 2012).

While *D. geminata* appears to have evolved mechanisms for nutrient uptake in oligotrophic streams that give it a competitive advantage over other algal species that proliferate in eutrophic conditions, other physiochemical conditions promote *D. geminata* mat growth, including altered hydrology (Kirkwood et al. 2009; Kumar et al. 2009). *D. geminata* appears well adapted to a wide range of hydrologic conditions, but recent studies noted that mats are common in stable channels with regulated flow regimes downstream of lakes and reservoirs (Kilroy et al. 2005; Kirkwood et al. 2009; Schweiger et al. 2011). Fewer high-flow events that scour the streambed or initiate bedload transport likely allow the long stalks in *D. geminata* mats to persist. However, the relative importance of flow regulation on the persistence of *D. geminata* mats has not been thoroughly investigated.

Although *D. geminata* mats are visually conspicuous and appear to spread quickly, there have been relatively few published studies that have examined effects of *D. geminata* on stream communities, especially macroinvertebrates and fish (e.g., Kilroy et al. 2009; James et al. 2010). Studies in New Zealand and Canada found *D. geminata* increased densities of oligochaetes, chironomids, trichopterans, and snails, but *D. geminata* has not been found to change overall macroinvertebrate diversity (Larned et al. 2007; Kilroy et al. 2009; Gillis and Chalifour 2010). Bickel and Closs (2008) showed that *D. geminata* did not affect oxygen concentrations in trout redds, but may have had a negative effect on trout spawning due to the modification of hydraulic exchange of water between the water column and hyporheic zone.

In New York State, *D. geminata* was first confirmed as a nuisance species in the Delaware river in the western Catskill mountains and in the Esopus Creek in the eastern Catskills following reports from anglers in 2009 (George and Baldigo, United States Geological Survey unpublished report). This appears to be the first documentation of *D. geminata* in the region, as no ecological records indicate *D. geminata* presence in the Catskills. *D. geminata* was absent from diatom samples from sites on the Esopus Creek in the eastern Catskills during 1999 and 2000 during surveys for benthic diatoms where *D. geminata* is now found (S. I. Passy, University of Texas at Arlington, personal communication). No subfossil evidence of *D. geminata* in the Catskills has yet been found; however, subfossil records show *D. geminata* as a rare species in Long Island, NY (Lohman 1939) and at the mouth of the Delaware river in New Jersey (Woolman 1894). Given the widespread distribution of *D. geminata* and the subfossil record at the mouth of watersheds that originate in the Catskills, we consider *D. geminata* to be a native invader in the Catskills region but, more importantly, a nuisance species that has rapidly spread with visually obvious cell and stalk proliferation in New York State.

Our research objective was to document temporal and spatial patterns of *D. geminata* cell abundance and mat

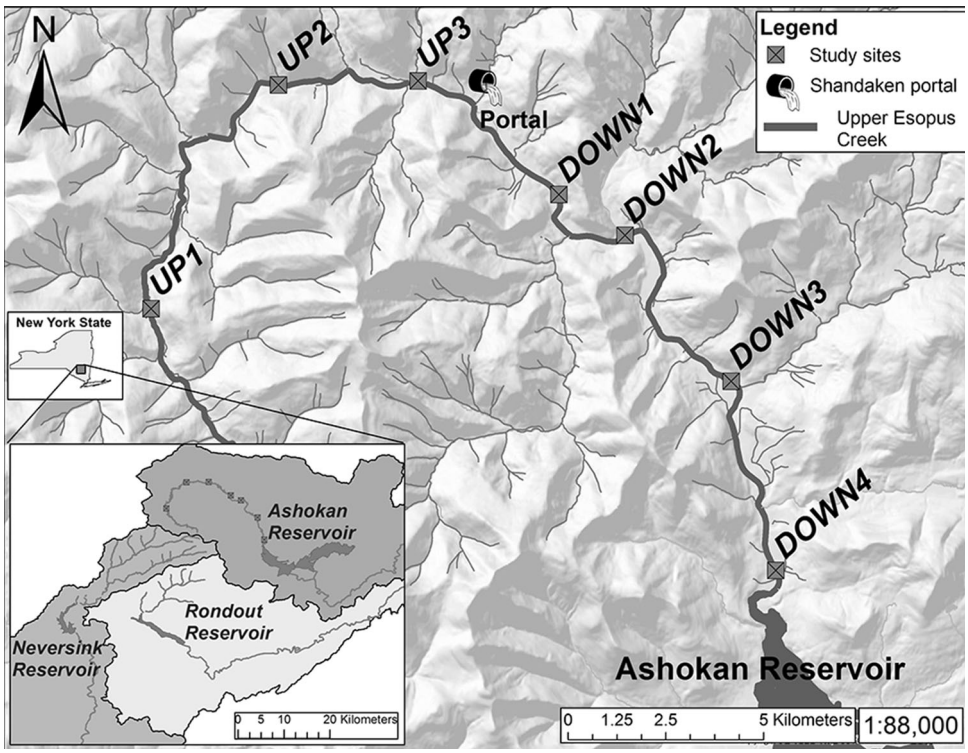

Fig. 1 Study sites in New York State (*smaller inset*), USA across Esopus, Neversink, and Rondout watersheds (*larger inset*) in the eastern Catskill mountains. In Esopus Creek (main map), sites were spaced along the mainstem of Esopus Creek from the upper Esopus headwaters to the mouth of the Ashokan reservoir. The Shandaken portal is an aqueduct that brings water from the Schoharie reservoir outflow

formation in eastern Catskill Mountain rivers, New York State, USA. Specifically, we asked if *D. geminata* ecology and nuisance characteristics were similar within its native range compared to other better known invasions such as in New Zealand (Larned et al. 2007) and western Canada (Kirkwood et al. 2009). We tested the following predictions generated from studies of non-native *D. geminata* invasions: (1) *D. geminata* will form larger nuisance mats and have higher cell abundance at locations below impoundments and reservoirs (e.g., Kirkwood et al. 2009). (2) *D. geminata* cover and cell density will be greater during time periods of stable, non-flashy flows and low sheer stress (Kirkwood et al. 2007). (3) *D. geminata* cell abundance and stalk production will be greater under oligotrophic conditions (e.g., Kilroy and Bothwell 2012). (4) *D. geminata* mats will have greater biomass and accumulation of phosphorus (P) than periphyton without *D. geminata*. (5) *D. geminata* mats will reduce macroinvertebrate community richness and biodiversity compared to other sites without *D. geminata* (e.g., James et al. 2010).

Methods

Study locations

Our study area included three adjacent watersheds in the eastern and southern Catskill mountains in eastern New York: Esopus Creek, Rondout Creek, and Neversink river. Hydrology in this region is complex, as all three streams have canals and reservoirs as part of the vast linked drinking water system for New York City (Arscott et al. 2006). Approximately 20 km downstream from Esopus Creek headwaters, water from the Shandaken tunnel (i.e., 'the portal'), a 29 km long interbasin-transfer aqueduct that diverts water from the adjacent Schoharie reservoir through a near-bottom release in a shallow edge of the reservoir, enters Esopus Creek (Fig. 1). Sampling locations for both the Rondout and Neversink were located on tributaries feeding into and directly below the bottom release outflow of each reservoir. In Esopus Creek, *D. geminata* mats were found upstream and downstream of the Schoharie reservoir outlet (i.e., the portal) in 2010–2012. In Rondout Creek, *D. geminata* mats were first discovered in 2011 below the reservoir, but not in reservoir tributaries. *D. geminata* was found at low cell densities upstream without clearly defined mats and downstream of the Neversink reservoir in 2011 and 2012.

Esopus Creek

As the target of *D. geminata* surveys focused on hydrologic and water chemistry variation, we selected seven sites that spanned 40 km along Esopus Creek above the Ashokan reservoir to sample on a weekly basis during the summers 2010–2012 (Fig. 1). Three sites were located upstream of

the Schoharie reservoir input (the portal), and four sites were downstream of this location. During autumn and spring, we sampled at two sites (Up 1 and Down 3) at a lower frequency to provide a seasonal record of *D. geminata* abundance in the creek. Within Esopus Creek, we surveyed multiple tributaries and other locations throughout the watershed on a one-time basis during summer 2011 and 2012.

Hydrologic measurements

At each site in Esopus Creek, we measured stream discharge along a transect perpendicular to flow by measuring water velocity (Marsh-Birney 2000-51, Frederick, MD, USA), width, and depth using standard methods (Turnipseed and Sauer 2010). We used a USGS gage (Coldbrook #01362500) for temporally explicit discharge measurements to quantify multiple aspects of hydrologic conditions at one site (Down 3). For the continuous discharge data, we calculated two annual metrics, discharge coefficient of variation and Richards–Baker flashiness index (R–B index). The latter measures oscillations in discharge relative to the cumulative discharge and indicates the flashiness of the flow during the time span (Eq. 2 in Baker et al. 2004). We quantified shear stress using USGS stage height data at 15 min intervals and the equation $\tau = \rho gRS$ where $\rho =$ density of water (1,000 kg/m), $g =$ gravitational acceleration (9.81 m/s), and $S =$ the slope (0.5 %) estimated over an 1,800 m reach surrounding our transect, and $R =$ the hydraulic radius approximated by average water depth. We calculated the relationship between mean water depth and USGS stage height as a linear function (mean depth $= 0.52 \times$ stage height $- 0.42$, $r^2 = 0.71$, $p < 0.001$) and used this relationship to calculate mean water depth. For each sampling date, we estimated the maximum antecedent shear stress from the previous 10 days. Finally, we calculated the critical shear stress, or the threshold for sediment transport, using the equation $\tau_c = \theta_c(\rho_s - \rho_w)gD$ (Lorang and Hauer 2003), where θ_c is the non-dimensional Shields stress parameter (0.06), ρ_s is the density of sediment (2,650 kg/m^3 for sandstone and shale), ρ_w is the density of water (1,000 kg/m^3), g is gravitational acceleration (9.81 m/s), and D is the median diameter of substrate (0.094 m as measured by Wolman pebble counts at site Down 3 from at least 50 substrate samples during the study period).

Water chemistry

We measured conductivity using a hand-held multi-meter (Hanna HI 98129, Woonsocket, RI, USA). We filtered 125 mL water through pre-ashed (480 °C for 4.5 h) glass fiber filters (Whatman 934-AH) in the field. Filtered samples were stored frozen until they were processed using ion chromatography. We also collected one 5 L water sample, which was transported back to the lab on ice within a few hours of collection. Within 24 h, we filtered three 0.5–1.5 L aliquots through pre-weighed and pre-ashed (480 °C for 4.5 h) glass fiber filters (Millipore AP40 with nominal pore size of 0.7 μm) with vacuum filtration for total particulate phosphorus (TPP) concentrations. Ion chromatography (Dionex ICS-3000, Sunnyvale, CA, USA) was used to measure sodium, potassium, magnesium, calcium, chloride, nitrate (NO_3^-), and sulfate (SO_4^{-3}) concentrations. Aliquots of filtered stream water (25 mL) for total dissolved phosphorus (TDP) analysis were digested with potassium persulfate and autoclaved for 30 min at 15 psi and 121 °C. Reagents (4.8 N sulfuric acid, ammonium molybdate, ascorbic acid, and potassium tartrate) were added to the autoclaved sample and TDP was quantified on a spectrophotometer (BioMate 6, Thermo Fisher Scientific, Waltham, MA, USA) at 880 nm after Murphy and Riley (1962) with a detection limit of ~3 μg/L. Total particulate phosphorus (TPP) concentrations were determined using the spectrophotometric method by submerging the filter in 25 mL of DI before treating with potassium persulfate.

Periphyton collection and analyses

We assessed benthic *D. geminata* cover along a transect placed perpendicular to stream flow. At one transect per site, we assessed the presence or absence of *D. geminata* and "other algae" at 10–20 evenly spaced intervals using visual and touch assessment. *D. geminata* is brown, has a wet cotton-like texture, and can be rolled into a ball, while other algae were generally green or brown and had a slippery texture. At some sites, we recorded the presence of both *D. geminata* and other algae as periphyton growth on *D. geminata* mats. All researchers were trained and tested to reduce subjectivity. In addition, we collected biofilm samples from six locations along each transect. We divided each transect into thirds and chose two rocks from random locations in each third (i.e., two from left bank, two from center, two from right bank). We scraped a geometric pattern (square or circle) that covered the majority of the rock surface using a wire brush until the rock was devoid of biofilm. Using a ruler, we measured the dimensions of the geometric pattern and calculated the cleared surface area on the rock. Rock scrapings from each pair of rocks were combined by rinsing into a 125 mL bottle and stored on ice until refrigerated.

Within 24 h of biofilm collection, we used aliquots from the biofilm samples to measure areal cover of *D. geminata* cells, biofilm ash-free dry mass (AFDM), and chlorophyll *a*, *b*, and *c*. Starting in June 2011, we estimated *D. geminata* cell density (cells/cm^2) for each rock scraping sample

by mixing a slurry of biofilm with 30 % hydrogen peroxide to dissolve extra-cellular material (1:3 volumetric ratio). The combined material was heated at 75 °C for 15 min and left standing for 1 h or until effervescence stopped (Bergey et al. 2010). Next, 1 mL of the mixture was pipetted onto a Sedgewick-Rafter cell counting chamber (Wildco Gridded Counting Chamber). *D. geminata* cells were counted at 100 × magnification in 20 randomly selected 1 µL boxes and scaled to cell densities using the ratio of the slurry to the total area of rocks scraped. *D. geminata* cell densities were averaged over the three samples at each transect. We filtered separate aliquots of the biofilm slurry through two different pre-weighed and pre-ashed (480 °C for 4.5 h) 47 mm glass fiber filters (Millipore AP40 with nominal pore size of 0.7 µm). One filter was dried at (70 °C for >24 h), reweighed, and then combusted (480° for 4.5 h) and re-weighed to calculate areal dry mass and ash-free dry mass (AFDM). Finally, the ashed filter, which included all the mat material and cells, was processed for total P using the procedure described above. We calculated the biofilm P (µg P/mg AFDM) by dividing the total P by the AFDM to get the proportion of P in *D. geminata* biofilms. The second filter was used for spectrophotometric chlorophyll (*a*, *b*, and *c*) analysis after hot ethanol extraction (see Richardson et al. 2009 for methods). Chlorophyll *a* occurs in most river algae, chlorophyll *b* only occurs in green algae and plants, and chlorophyll *c* is found in all diatoms (Ritchie 2008). We calculated the ratio of chlorophyll *b* to chlorophyll *c* with lower chlorophyll *b*:*c* ratios indicating greater dominance by diatoms in the algal community.

Benthic macroinvertebrates

In summer 2011 and 2012, we collected samples for macroinvertebrates at 10 sites that spanned a range of *D. geminata* densities above and below the portal in the Esopus Creek and reservoir outlets in Neversink and Rondout watersheds. We followed protocols for stream macroinvertebrate sampling in New York (NYS DEC 2012). Benthic samples were collected from each site using a 500 µm nylon mesh kick net by disturbing the substrate upstream of the net by foot and continuing over a 5 m transect for 5 min (Bode et al. 2002). Samples were preserved in 95 % ethanol and then sub-sampled in the lab by randomly selecting 15 cm^3 from the sample, removing a minimum of 100 individuals. Macroinvertebrates were identified to family level. We calculated total family richness and the Shannon Wiener (H') index for biodiversity (Shannon 1948). For each macroinvertebrate collection site, we measured *D. geminata* cell abundance from rock scrapings at three locations according to protocols described above.

Statistical analyses

We compared *D. geminata* cell densities above and below reservoir outlets using two sample *t* tests. We used two-way ANOVAs to compare *D. geminata* cover and water chemistry variables with year and sampling site as factors. We transformed *D. geminata* cell densities to account for non-normal distribution (i.e., natural log (ln) of cell densities +1). Multiple comparisons were tested following a significant ANOVA using Tukey's honestly significant difference test. Linear regression was used to identify relationships between *D. geminata* cell densities and total water column P, biofilm AFDM, biofilm P, chlorophyll *a,* and antecedent shear stress. We used least-squares linear regression between *D. geminata* cover and ln transformed *D. geminata* density (ln+1) to determine if *D. geminata* cover could predict cell density. We calculated Pearson's correlation coefficients to compare metrics of *D. geminata* abundance including cell density, AFDM, and % cover with water chemistry, and other algal cover. For macroinvertebrate communities, we used Pearson's correlation coefficients to compare *D. geminata* density with family richness and biodiversity with a Bonferroni correction (per comparison $\alpha = 0.025$). Finally, we compared metrics of *D. geminata* abundance including cell density, AFDM, and % cover across sites where the TDP was above and below our detection limit of ~3 µg/L. All statistical analyses were conducted using the R statistical package (R Development Core Team 2009).

Results

Spatial and temporal extent of D. geminata mat cover

D. geminata cover increased with distance downstream in Esopus Creek. However, total cover was different among the 3 years (two-way ANOVA interaction: $F_{10,76} = 2.46$, $p = 0.013$). In 2010 and 2012, the relative benthic cover of *D. geminata* approached 100 %, but sites were covered only to a maximum of ~50 % in 2011 (Fig. 2a). The most upstream site showed very little cover in all 3 years. *D. geminata* cell density reflected similar spatial and temporal patterns to percent cover. At downstream sites, maximum cell density in 2012 was >2 orders of magnitude higher than 2011 (Fig. 2b).

In both Esopus and Rondout Creeks, *D. geminata* cell density was significantly higher below the reservoirs compared to upstream (Table 1). No *D. geminata* was found in tributaries upstream of Rondout Creek reservoir (Table 1). In the Neversink river, we found no clearly identifiable mats, but *D. geminata* was present at low

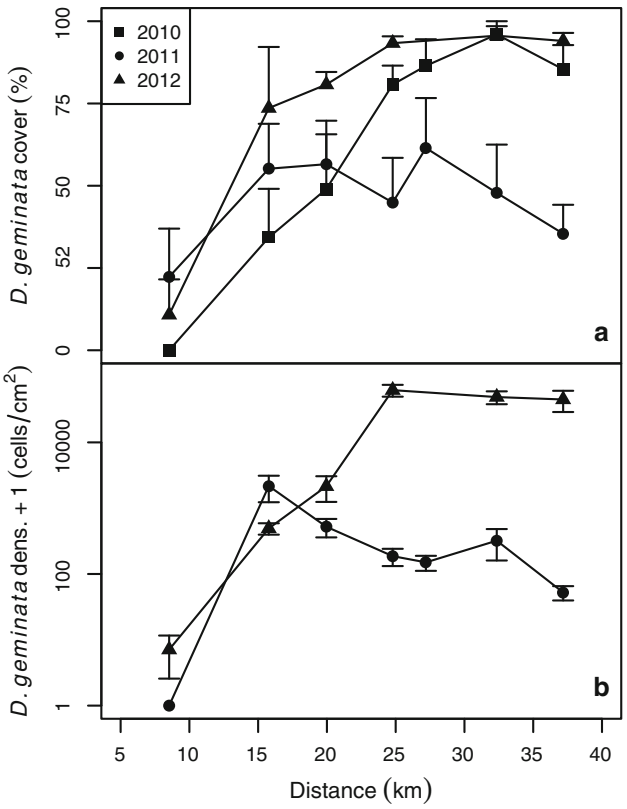

Fig. 2 Longitudinal patterns of **a** mean (+SE) *D. geminata* cover (%) and **b** mean (±SE) *D. geminata* density (cells/cm^2) in Esopus Creek over the 3 year study period. *D. geminata* density was transformed as ln(density + 1) to account for 0 cell density measurements

densities in biofilm samples taken above and below its reservoir.

Discharge patterns in Esopus Creek varied among years and were negatively correlated with *D. geminata* density. In 2011, tropical storms Irene and Lee passed directly through the Catskills contributing to high flows in late August and early September (Fig. 3a). 2011 had the wettest August, September, and October over a >100 year record (Klug et al. 2012). Stream flow in 2011 was extremely variable, with high coefficient of variation and indices of flashiness relative to 2010 and 2012 (Table 2). Mean *D. geminata* density was <1,000 cells/cm^2 during the summer and fall in 2011. In contrast, summer 2012 was drier, and discharge was more stable as indicated by lower flashiness indices (Table 2). *D. geminata* density peaked at ~100,000 cells/cm^2 during mid-summer 2012 (Fig. 3b). Cell density was negatively related to the maximum antecedent shear stress during the 10 days prior to the cell density measurement [ln(cell density + 1) = $-0.27 \times$ antecedent $\tau + 13.5$, $r^2 = 0.54$, $p < 0.001$; Fig. 4]. The only time shear stress exceeded critical values (i.e., when bed sediments were mobilized) was late summer 2011: Tropical Storm Irene on August 28 (maximum shear stress = 162 N/m^2), Tropical Storm Lee on September 7, and an unnamed storm on September 28.

We averaged the *D. geminata* density and benthic cover for each site during the summer field season for 2011 and 2012. We only collected data from one site outside the growing season (DOWN3) and excluded that data from the analysis. *D. geminata* density and benthic cover were positively related to each other across several orders of magnitude [ln(cell density + 1) = $0.11 \times$ cover $- 0.38$, $p < 0.001$, $r^2 = 0.87$; Fig. 5]. The maximum mat thickness was highly variable. We found some tendrils of stalk material that exceeded 15 cm but we consistently saw mats >1.5 cm in 2010 and 2012.

Water chemistry, biofilms, and D. geminata

Several water chemistry variables followed longitudinal patterns of *D. geminata* in Esopus Creek. The most upstream site, where *D. geminata* was absent or at low density, had the lowest conductivity ($F_{6,130} = 4.4$, $p < 0.001$), calcium ($F_{6,117} = 7.0$, $p = 0.03$), sodium ($F_{6,117} = 8.1$, $p < 0.001$), and chloride concentrations ($F_{6,117} = 5.2$, $p < 0.001$), and also the highest NO_3^- concentrations ($F_{6,117} = 9.9$, $p < 0.001$). In addition, NO_3^- concentration was higher in 2012 than in 2011 and 2010 ($F_{2,130} = 5.2$, $p < 0.001$). Across all sites, *D. geminata* cell density was positively correlated with conductivity ($r = 0.89$, $p < 0.001$) and calcium concentrations ($r = 0.83$, $p < 0.001$). Similarly, *D. geminata* cover was positively correlated with conductivity ($r = 0.8$, $p < 0.001$) and calcium concentration ($r = 0.69$, $p < 0.001$). *D. geminata* metrics were not correlated with SO_4^{-3} concentration. *D. geminata* cover was negatively related to NO_3^- concentration ($r = -0.52$, $p = 0.01$). *D. geminata* cell density was positively related to total water column P (TDP) ($r = 0.28$, $p = 0.006$), but this relationship explained little variation. TDP was low in Esopus Creek (10.5 µg/L ± 1.7 SE), but these values and the preceding correlations do not include multiple values that fell below our detection limits. Locations with TDP lower than detection limits had similar cell densities to those with measurable TDP ($t = 1.54$, $df = 69$, $p = 0.12$) but had significantly higher *D. geminata* cover ($t = 2.03$, $df = 100$, $p = 0.04$). Ratios of chlorophyll *b*:*c* (green algae to diatoms) in periphyton were negatively correlated with *D. geminata* cell density ($r = -0.45$, $p < 0.001$). Finally, the *D. geminata* cover was negatively correlated to algal cover ($r = -0.23$, $p = 0.017$).

D. geminata cell density was positively related to biofilm dry mass [dry mass = $3 \times 10^{-4} \times$ ln(cell density + 1) + 3.7, $p < 0.001$, $r^2 = 0.76$], AFDM [AFDM = $2 \times 10^{-5} \times$ ln(cell density + 1) + 0.48, $p < 0.001$, $r^2 = 0.80$; Fig. 6a], and biofilm P [biofilm P = $4 \times 10^{-4} \times$ ln(cell density + 1) + 11.3, $p < 0.001$; $r^2 = 0.59$; Fig. 6b]. Similarly, *D. geminata* cell density was positively related to biofilm

Table 1 *D. geminata* cell density (mean ±SE) in study sites of the Catskill mountains, NY (2011–2012) relative to reservoir locations

Watershed	Reservoir	Density above reservoir (cells/cm^2)	Density below reservoir (cells/cm^2)	*t* test
Esopus	Schoharie	821.0 ± 244	25,052 ± 4,464.3	$p < 0.001$, $t = -5.5$, $df = 85$
Rondout	Rondout	Absent	757 ± 392.2	$p < 0.001$, $t = -6.6$, $df = 20$
Neversink	Neversink	3.4 ± 3.0	6.0 ± 4.1	$p = 0.59$, $t = -0.54$, $df = 17$

chlorophyll *a* [chl $a = 1 \times 10^{-4} \times \ln(\text{cell density} + 1) + 1.6$, $p < 0.001$, $r^2 = 0.50$, Fig. 6c] and chlorophyll *c* [chl $c = 2 \times 10^{-4} \times \ln(\text{cell density} + 1) + 0.35$, $p < 0.001$, $r^2 = 0.47$] concentrations.

Macroinvertebrates and D. geminata

Thirty-seven families of macroinvertebrates from 10 orders were collected. The most common taxa collected, i.e., found in most or all of the samples, include Chironomidae (Diptera), Baetidae (Ephemeroptera), Ceratopogonidae (Diptera), and Hydropsychidae (Trichoptera). Total family richness ranged between 6 and 19 families and H′ ranged from 1.18 to 2.49. *D. geminata* cell density was negatively correlated with total family richness ($r = -0.77$, $p = 0.024$; Fig. 7) and was negatively related to but not significantly correlated with H' ($r = -0.68$, $p = 0.030$; Bonferroni correction was $\alpha = 0.025$). At several of the sites with the highest *D. geminata* density, no Trichoptera or Plecoptera individuals were found. With increasing *D. geminata* density, several families were lost from samples including Leptophlebiidae (Ephemeroptera), Leuctridae (Plecoptera), and Brachycentridae (Trichoptera).

Discussion

We consider *D. geminata* to be a native invader in the Catskills due to its widespread distribution and presence in subfossil records from the Delaware river, which is downstream of the Catskills. However, we found *D. geminata*'s ecology and nuisance characteristics in the Catskills to be similar in several ways to those locations where it is a well-known invasive species; for example, in New Zealand (Larned et al. 2007) and western Canada (Kirkwood et al. 2007, 2009). Specifically, we found (1) higher *D. geminata* cell density below reservoirs compared to upstream except in the Neversink system; (2) *D. geminata* mats developed in low nutrient conditions; (3) higher *D. geminata* cell density was associated with higher intra-mat P. However, we also found several important ecological characteristics. First, *D. geminata* mats and cell densities were lower in times with unstable, flashy flow and high shear stress. Second, macroinvertebrate community indices were negatively correlated with *D. geminata* cell densities which is in contrast with observations reported by Larned et al. (2007) for *D. geminata* invasions in New Zealand. These findings are important steps towards developing management strategies for this nuisance species.

Hydrologic controls

D. geminata is often found in abundance below lake outflows, reservoirs, or impoundments where stream flows are heavily regulated and benthic substrates are typically stable (Table 1; Kirkwood et al. 2009; Schweiger et al. 2011). Our study coincidentally captured the influence of two tropical storms, and clearly demonstrated that flood intensity was negatively correlated with *D. geminata* density and cover. To our knowledge, the highest *D. geminata* cell densities ever reported (>10^5 cells/cm^2; Fig. 3) were measured during the low and stable flow periods in summer 2012 in Esopus Creek. During this time, we observed *D. geminata* growing on a variety of substrates including grasses, rocks, and silt. These data suggest *D. geminata* mats are susceptible to increases in shear stress through scouring of periphyton communities (Table 2; Fig. 4; Kilroy et al. 2005; Kirkwood et al. 2007; Miller et al. 2009). Strong hydrodynamic forces can scour mats off in-stream surfaces, increase mat abrasion by suspended particles, or mobilize all bed sediments (Cullis et al. 2012). When hydrodynamic forces erode or penetrate well-developed mats, we observed the mat acting as a 'sail' where large clumps were lifted off the streambed. In Esopus Creek, shear stress exceeded critical shear stress only three times during our study, so it appears most of the less severe storms removed *D. geminata* mats from the rocks via lift and drag or abrasive forces rather than through mobilization of bed sediments.

Unexpectedly, thick *D. geminata* growth occurred at locations with water velocity up to 1.5 m/s, near the maximum velocity where we could safely stand and sample the benthic surface. It appears that high *variation* in velocity, rather than high velocity itself, controls scour and regrowth patterns (Fig. 3; Spaulding and Elwell 2007). Overall, the *D. geminata* response to hydrology may have

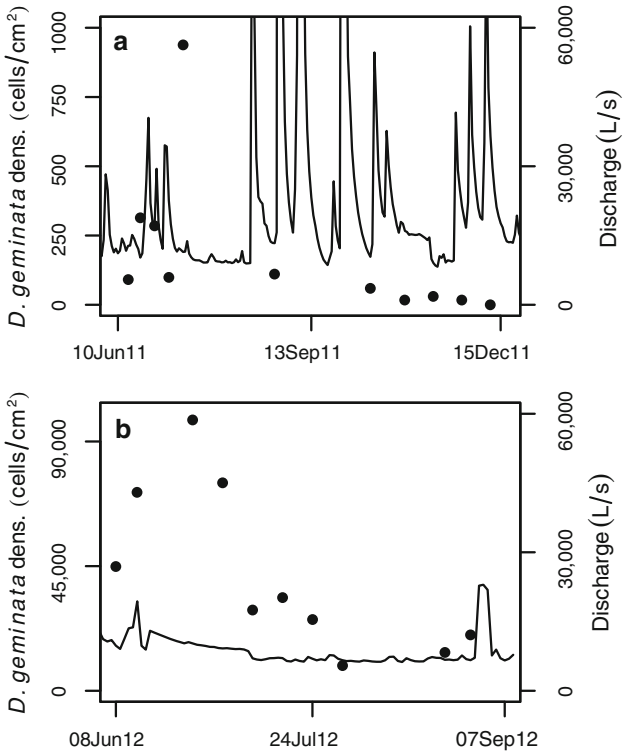

Fig. 3 *D. geminata* density at site Down 3 (*closed circles*) and daily discharge from USGS gage in Esopus Creek at Cold Brook, NY (*solid line*) during summer in **a** 2011 and **b** 2012. Note the large scale difference between years for *D. geminata* density

Table 2 Discharge and *D. geminata* at site "Down 3" in Esopus Creek 2010–2012

Year	Sampling dates	R–B index	Discharge CV (%)	*D. geminata* cover (%)	*D. geminata* density (cells/cm^2)
2010	14 Jun to 03 Sep	0.16	60	96.0 ± 4.0	ND
2011	08 Jun to 13 Dec	0.60	229	47.8 ± 14.7	320 ± 161
2012	01 Jun to 02 Sep	0.13	48	95.6 ± 2.9	48,842 ± 10,824

Richards–Baker Flashiness index (R–B index) and the coefficient of variation (CV) of discharge indicate the variability of flow. *D. geminata* cover and density were averaged during each year of study. *ND* (no data) indicates cell densities were not measured

implications for bloom management. For example, downstream of impoundments, short pulses of water mimicking small-to-moderate storm flows could potentially be used to minimize bloom size, and larger pulses could scour the bed sediments and more completely remove mats and have a potentially longer lasting negative effect on mat proliferation (Kirkwood et al. 2009; Miller et al. 2009; Cullis et al. 2012).

Water chemistry and D. geminata

In our study and elsewhere, *D. geminata* proliferation and stalk production occurred in locations with low water column nutrients (Bothwell et al. 2012; Kilroy and Bothwell 2012; James et al. 2014). Cullis et al. (2012) hypothesized *D. geminata* mats decrease with higher P concentrations because the stalks are an evolutionary adaptation that allows the diatom to obtain and retain nutrients in oligotrophic conditions (Ellwood and Whitton 2007). However, under eutrophic conditions, the stalk production becomes an energetic expense rather than an asset. There are several proposed mechanisms for P uptake

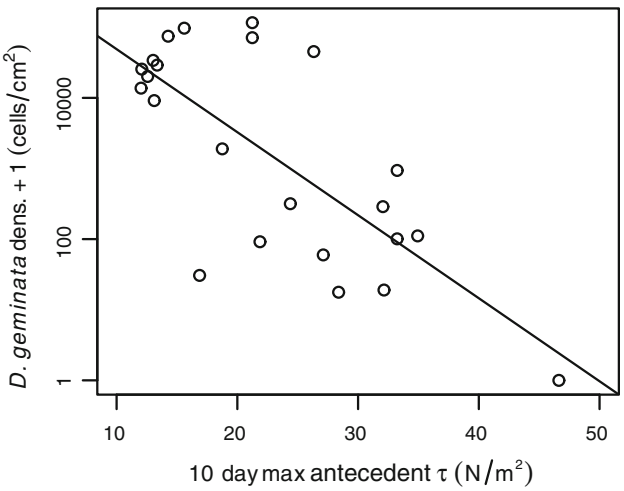

Fig. 4 Least-squared linear regression between *D. geminata* cell density (ln transformed) and the maximum antecedent shear stress from the 10 days preceding the cell density measurement ($r^2 = 0.71$, $p < 0.001$)

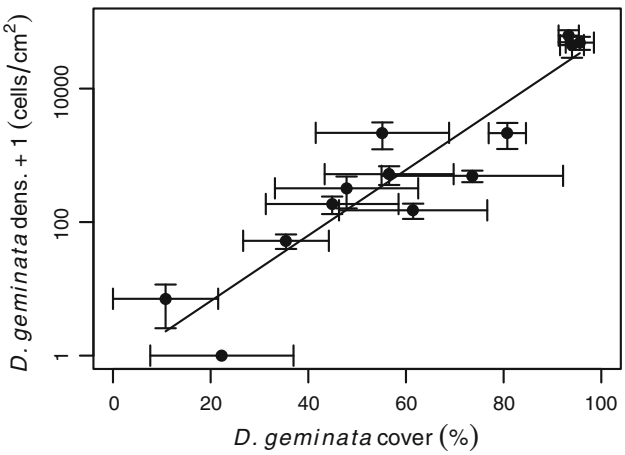

Fig. 5 Least-squared linear regression between *D. geminata* cover vs. *D. geminata* cell density (ln transformed) ($r^2 = 0.87$, $p < 0.001$). Each point represents the mean (±SE) of one site for 1 year (2011–2012)

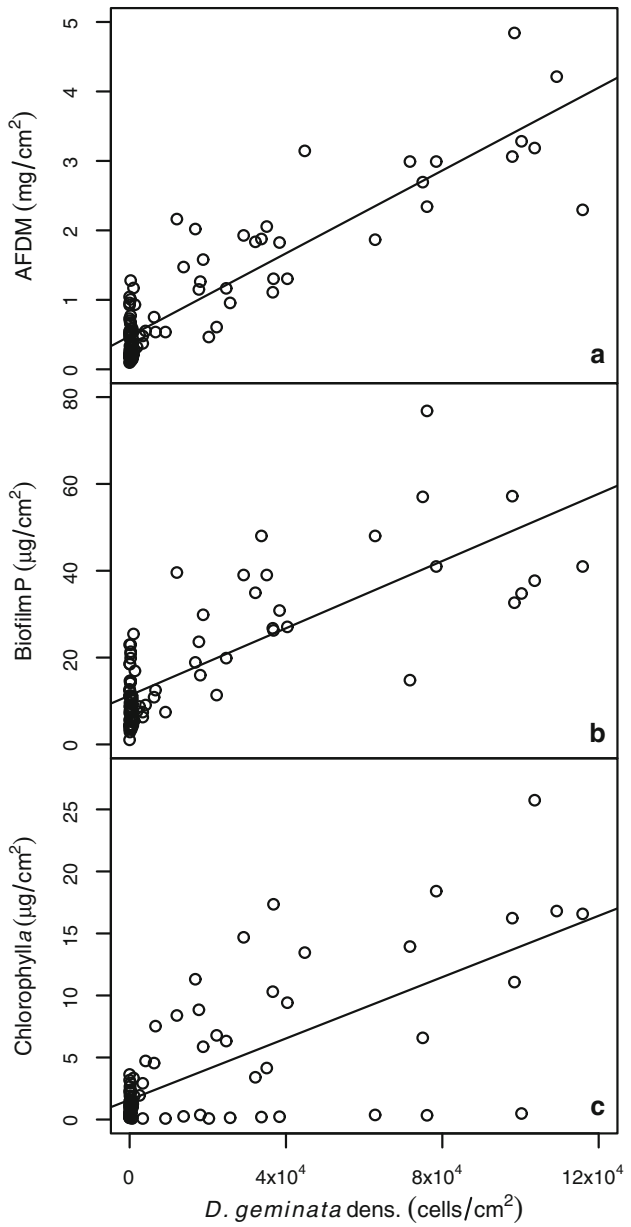

Fig. 6 Least-squared linear regressions between *D. geminata* cell density and biofilm **a** ash free dry mass ($r^2 = 0.80$, $p < 0.001$), **b** biofilm phosphorus ($r^2 = 0.59$, $p < 0.001$), and **c** chlorophyll *a* ($r^2 = 0.50$, $p < 0.001$)

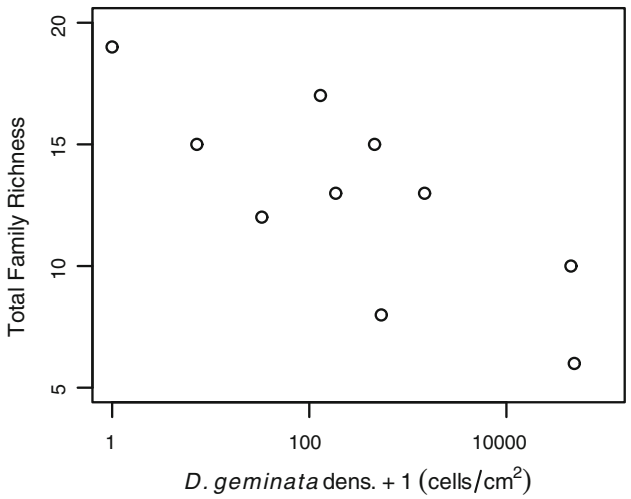

Fig. 7 Correlation between *D. geminata* cell density (ln transformed) and total macroinvertebrate family richness for 10 sites from 2011 and 2012 ($r = -0.77$, $p = 0.024$). Each point represents mean *D. geminata* densities from the year at that location

that enable *D. geminata* growth in P-limited oligotrophic waters (Bott et al. 2006). Sundareshwar et al. (2011) proposed *D. geminata* enhanced P uptake via reducing conditions within the anoxic mats, which release Fe-bound P. The P is then available for uptake by *D. geminata* cells in the overlying oxic zone.

Our study did not examine intra-mat biogeochemical transformations, but *D. geminata* mats with high cell densities and high AFDM had higher intra-mat P than mats with low cell densities or periphyton that did not contain *D. geminata* (Fig. 6b). This suggests *D. geminata* enhanced P sequestration within mats, possibly through the stalks promoting direct water column P uptake (Ellwood and Whitton 2007) or through the Fe-reduction pathway suggested by Sundareshwar et al. (2011). However, water column SO_4^- concentrations were not correlated with *D. geminata* density (DCR, unpublished data), and Bothwell et al. (2012) found that Fe concentrations did not affect *D. geminata* P uptake. We acknowledge that Fe, S, and P redox changes occurring on micro-scales within *D. geminata* mats may not be reflected in measurements of water column solute concentrations. In addition, we note that higher P in *D. geminata* mats could be the product of captured sediment which contains organic P and adsorbed inorganic P (Ellwood and Whitton 2007; Sundareshwar et al. 2011).

D. geminata was negatively related to water column N concentrations at our study sites, a pattern which has recently been found elsewhere (Schweiger et al. 2011). One explanation for this relationship is that under eutrophic conditions, *D. geminata* is outcompeted for nutrients and substrate by rapidly growing algal species including common diatoms in Esopus Creek such as *Achnanthes* spp. (S. I. Passy, University of Texas at Arlington, personal communication) and green algae including *Cladophora glomerata* or *Spirogira* spp. (e.g., Biggs 2000; Dodds et al. 2002; Dodds 2006). However, *D. geminata* cell production may be correlated with low water column N concentrations because of high N demand. *D. geminata* cells and other biofilm organisms that live in the mats take up N from the water column through assimilatory or dissimilatory pathways (i.e., denitrification). *D. geminata* and N may be

unrelated and merely following opposite seasonal patterns. However, the demand for N by *D. geminata* mats relative to periphyton with no *D. geminata* is unknown, as no measurements of N uptake in the mats have been completed. Determining whether the negative relationship between *D. geminata* and water column N is due to competition among periphyton taxa, or through high N demand of organisms in the *D. geminata* mats will require further research.

Solutes other than N and P may also drive *D. geminata* growth. Rost et al. (2011) found that calcium concentration was positively correlated to the presence of *D. geminata* in streams, and we found the same pattern in Esopus Creek. Calcium is important for adhesion of diatoms to their substrate (Geesey et al. 2000) and this could be critical to *D. geminata* mat formation. However, calcium concentrations may be linked to pH or dissolved inorganic carbon and could indirectly affect *D. geminata* by regulating the availability of nutrients such as P through calcite precipitation (Diaz et al. 1994; Whitton et al. 2009).

Effect on macroinvertebrates

In this study, *D. geminata* density was negatively correlated with total family richness (Fig. 7). James et al. (2010) also found a lower proportion of EPT taxa in streams with *D. geminata* present in South Dakota. In contrast, other studies have shown *D. geminata* was positively correlated with total invertebrate density, driven mostly by increases in chironomids and oligochaetes, with no effect on species composition (Kilroy et al. 2009; Gillis and Chalifour 2010). *D. geminata* density in this study ranged over several orders of magnitude (Fig. 7), more than reported in previous studies (Kilroy et al. 2009; Gillis and Chalifour 2010). It appears this large variation provided the range of *D. geminata* density needed to document the relationship with reduced macroinvertebrate richness. *D. geminata* mats, especially during large blooms, can favor clinging or burrowing macroinvertebrates (e.g., chironomids and baetid mayflies, James et al. 2010) or those tolerant of low oxygen like chironomids or oligochaetes (Gillis and Chalifour 2010). Thick mats could reduce near bed dissolved oxygen, create poor hydraulic exchange with the water column (Bickel and Closs 2008), and reduce viable habitat. Although this has not yet been explicitly tested, the sulfated polysaccharides stalk material that comprises most of the mat biomass is likely unpalatable for both microbes and macroinvertebrates.

D. geminata mat biomass

Using data from a New York City drinking water supply monitoring program, we were in the unique position to assess *D. geminata* impact on benthic periphyton biomass. Bott et al. (2006) sampled Esopus Creek in 2000–2002 prior to the appearance of nuisance *D. geminata* mats at one location downstream of the portal, near site Down 1 (Fig. 1). At that time, no *D. geminata* mats were present, and biofilm AFDM and chlorophyll *a* in Esopus Creek was $\sim$0.7 mg AFDM cm^{-2} and $\sim$5 µg chlorophyll *a* cm^{-2}, respectively (Bott et al. 2006). These values are comparable to sites in the present study where *D. geminata* was absent (Fig. 6a, c). However, post *D. geminata* mat appearance, biofilm AFDM and chlorophyll *a* at the same site were up to 10 times greater (Fig. 6a, c). This is similar to results for biofilm biomass before and after *D. geminata* invasion in a New Zealand stream (Kilroy et al. 2009).

The high biomass of *D. geminata* mats relative to non-*D. geminata* containing periphyton can affect the timing, quality, and quantity of carbon (C) retention patterns in streams. In biofilms <1 mm thick, extracellular polysaccharides can enhance retention of suspended particles, increase hydrodynamic storage zones, and increase nutrient uptake (Battin et al. 2003). Because *D. geminata* biofilm mats were >10 cm thick at some sites, and the majority of the biofilm mass is carbon-rich extracellular material, these mats are likely to have the same or greater influence on C retention as other periphyton and bacterial driven stream biofilms in two ways. First, the *D. geminata* mats represent a large fraction of the streams' autochthonous fixed C. Second, the mats can provide enhanced habitat for heterotrophic microorganisms that may remove allochthonous C from the water column and the mats may retain allochthonous C in the form of leaves or organic carbon adsorbed to clays and silts. As the mats are typically scoured during floods, this generates pulsed outputs of C which could affect both biofilm consumers in higher trophic levels as well as downstream ecosystems.

Conclusions

Didymosphenia geminata is most likely a native invader in Catskill Mountain streams, and its newly documented mat development patterns have a striking visual appearance and high biomass. *D. geminata* generates large mats in otherwise oligotrophic ecosystems, which negatively affects macroinvertebrate taxon richness. High variability in flooding reduces *D. geminata* bloom size and density, which may present an opportunity for mitigating its effect and predicting its abundance as it appears in new locations. Water column NO_3^- and *D. geminata* abundance were negatively correlated, but a mechanistic explanation for the relationship requires further investigation. A combination of physiochemical factors is likely to dictate why *D. geminata* generates nuisance mats especially below

reservoir outflows in Catskill Mountain streams. A greater understanding of why *D. geminata* cells and mats propagate and how mats affect ecosystem function (i.e., nutrient budgets and secondary production) is needed. Our results, in combination with future studies, may help devise new strategies to mitigate effects of *D. geminata* invasion and limit its ongoing range expansion both as a non-native and native invasive species.

Acknowledgments This research was funded by grants from the New York State Water Resources Institute and New York State Department of Environmental Conservation Hudson River Estuary Program, Cornell Cooperative Extension of Ulster County Ashokan Watershed Stream Management Program, SUNY New Paltz Summer Undergraduate Research Experience, and U.S. National Science Foundation (EAR0851022) to S. Chowdhury and J. Rayburn. Initial water chemistry analysis was supported by a grant to T. Hoellein, C. Zarnoch, and D. Gruber from the National Science Foundation (MRI0959876). We thank summer REU students and interns, L. Achterberg, E. Bialowas, A. Handler, A. Miller, M. Redfield, and N. Rigolino, for driving data collection. We appreciate additional field and lab help from E. Arnold, S. Beirne, C. Carey, D. Hodder, A. Jacobs, T. Maxwell, M. Sandstrom, A. Shimizu, S. Steeneck, and M. Weber. We thank D. Davis (NY Department of Environmental Protection), E. Higgins (Cornell Cooperative Extension), and A. Gearwar (United States Geological Survey) for guidance, data, and general project assistance. We thank Scott George and anonymous reviewers for suggestions that improved earlier versions of this manuscript.

References

Aboal M, Marco S, Chaves E, Mulero I, Garcia-Ayala A (2012) Ultrastructure and function of stalks of the diatom *Didymosphenia geminata*. Hydrobiologia 695:17–24

Arscott DB, Dow CL, Sweeney BW (2006) Landscape template of New York City's drinking-water-supply watersheds. J N Am Benthol Soc 25:867–886

Baker DB, Richards RP, Loftus TT, Kramer JW (2004) A new flashiness index: characteristics and application to Midwestern rivers and streams. J Am Water Resour Assoc 40:503–522

Battin TJ, Kaplan LA, Newbold JD, Hansen CME (2003) Contributions of microbial biofilms to ecosystem processes in stream mesocosms. Nature 426:439–442

Bergey EA, Cooper JT, Phillips BC (2010) Substrate characteristics affect colonization by the bloom-forming diatom *Didymosphenia geminata*. Aquat Ecol 44:33–40

Bickel TO, Closs GP (2008) Impact of *Didymosphenia geminata* on hyporheic conditions in trout redds: reason for concern? Mar Freshw Res 59:1028–1033

Biggs BJF, Kilroy C (2000) Stream periphyton monitoring manual. New Zealand Ministry of the Environment, Christchurch, New Zealand. Available online: http://www.niwa.co.nz/our-science/freshwater/tools/periphyton. Accessed 14 Feb 2013

Blanco S, Ector L (2009) Distribution, ecology and nuisance effects of the freshwater invasive diatom *Didymosphenia geminata* (Lyngbye) M. Schmidt: a literature review. Nova Hedwigia 88:3–4

Bode RW, Novak MA, Abele LE, Heitzman DL, Smith AJ (2002) Quality assurance work plan for biological stream monitoring in New York State, New York State Department of Environmental Conservation technical report

Bothwell ML, Kilroy C, Taylor BW, Ellison ET, James DA, Gillis CA, Bladon KD, Silins U (2012) Iron is not responsible for *Didymosphenia geminata* bloom formation in phosphorus-poor rivers. Can J Fish Aquat Sci 69:1723–1727

Bott TL, Montgomery DS, Newbold JD, Arscott DB, Dow CL, Aufdenkampe AK, Jackson JK, Kaplan LA (2006) Ecosystem metabolism in streams of the Catskill mountains (Delaware and Hudson river watersheds) and lower Hudson valley. J N Am Benthol Soc 25:1018–1044

Carey MP, Sanderson BL, Barnas KA, Olden JD (2012) Native invaders-challenges for science, management, policy, and society. Front Ecol Environ 10:373–381

Cleve PT (1965) Synopsis of the naviculoid diatoms. Kongliga Sevenska Vetenskaps-Akademiens Handlingar, Stockholm. Reprinted from 1894–1896

Cullis JDS, Gillis CA, Bothwell ML, Kilroy C, Packman A, Hassan M (2012) A conceptual model for the blooming behavior and persistence of the benthic mat-forming diatom *Didymosphenia geminata* in oligotrophic streams. J Geophys Res 117:G00N03

Diaz OA, Reddy KR, Moore PA (1994) Solubility of inorganic phosphorus in stream water as influenced by pH and calcium concentration. Water Res 28:1755–1763

Dodds WK (2006) Eutrophication and trophic state in rivers and streams. Limnol Oceanogr 51:671–680

Dodds WK, Smith VH, Lohman K (2002) Nitrogen and phosphorus relationships to benthic algal biomass in temperate streams. Can J Fish Aquat Sci 59:865–874

Drake DAR, Mandrak NE (2010) Least-cost transportation networks predict spatial interaction of invasion vectors. Ecol Appl 20:2286–2299

Ehrenfeld JG (2010) Ecosystem consequences of biological invasions. Annu Rev Ecol Syst 41:59–80

Ellwood NTW, Whitton BA (2007) Importance of organic phosphate hydrolyzed in stalks of the lotic diatom *Didymosphenia geminata* and the possible impact of atmospheric and climatic changes. Hydrobiologia 592:121–133

Flöder S, Kilroy C (2009) *Didymosphenia geminata* (Protista, Bacillariophyceae) invasion, resistance of native periphyton communities, and implications for dispersal and management. Biodivers Conserv 18:3809–3824

Geesey GG, Wigglesworth-Cooksey B, Cooksey KE (2000) Influence of calcium and other cations on surface adhesion of bacteria and diatoms: a review. Biofouling 15:195–205

Gillis CA, Chalifour M (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

James DA, Ranney SH, Chipps SR, Spindler BD (2010) Invertebrate composition and abundance associated with *Didymosphenia geminata* in a montane stream. J Freshw Ecol 25:235–241

James DA, Mosel K, Chipps SR (2014) The influence of light, stream gradient, and iron on *Didymosphenia geminata* bloom development in the Black Hills, South Dakota. Hydrobiologia 72:117–127

Kilroy C, Bothwell ML (2012) *Didymosphenia geminata* growth rates and bloom formation in relation to ambient dissolved phosphorus concentration. Freshw Biol 57:641–653

Kilroy C, Unwin M (2011) The arrival and spread of the bloom-forming freshwater diatom *Didymosphenia geminata* in New Zealand. Aquat Invasions 6:249–262

Kilroy C, Snelder T, Sykes J (2005) Likely environments in which the non-indigenous freshwater diatom, *Didymosphenia geminata*, can survive, in New Zealand, NIWA Consultancy report 2005-043, For biosecurity New Zealand

Kilroy C, Larned ST, Biggs BJF (2009) The non-indigenous diatom *Didymosphenia geminata* alters benthic communities in New Zealand rivers. Freshw Biol 54:1990–2002

Kirkwood AE, Shea T, Jackson LJ, McCauley E (2007) *Didymosphenia geminata* in two Alberta headwater rivers: an emerging invasive species that challenges conventional views on algal bloom development. Can J Fish Aquat Sci 64:1703–1709

Kirkwood AE, Jackson LJ, McCauley E (2009) Are dams hotspots for *Didymosphenia geminata* blooms? Freshw Biol 54:1856–1863

Klug JL, Richardson DC, Ewing HA, Hargreaves BR, Samal NR, Vachon D, Pierson DC, Lindsey AM, O'Donnell DM, Effler SW, Weathers KC (2012) Ecosystem effects of a tropical cyclone on a network of lakes in northeastern North America. Environ Sci Technol 46:11693–11701

Kumar S, Spaulding SA, Stohlgren TJ, Hermann KA, Schmidt TS, Bahls LL (2009) Potential habitat distribution for the freshwater diatom *Didymosphenia geminata* in the continental US. Front Ecol Environ 7:415–420

Larned S, Arscott DB, Blair N, Jarvie B, Jellyman D, Lister K, Schallenberg M, Sutherland S, Vopel K, Wilcock B (2007) Ecological studies of *Didymosphenia geminata* in New Zealand, 2006–07, NIWA Client report: CHC2007-070

Larned ST, Packman AI, Plew DR, Vopel K (2011) Interactions between the mat-forming alga *Didymosphenia geminata* and its hydrodynamic environment. Limnol Oceanogr Fluids Environ 1:4–22

Lavery JM, Kurek J, Rühland KM, Gillis CA, Pisaric MFJ, Smol JP (2014) Exploring the environmental context of recent *Didymosphenia geminata* proliferation in Gaspésie, Quebec, using paleolimnology. Can J Fish Aquat Sci 71:1–11

Lohman KE (1939) Pleistocene diatoms from Long Island, New York. U.S. Geol Surv Prof Pap 189:229–235

Lorang MS, Hauer FR (2003) Flow competence and streambed stability: an evaluation of technique and application. J N Am Benthol Soc 22:475–491

Miller MP, McKnight DM, Cullis JD, Greene A, Vietti K, Liptzin D (2009) Factors controlling streambed coverage of *Didymosphenia geminata* in two regulated streams in the Colorado front range. Hydrobiologia 630:207–218

Murphy J, Riley PA (1962) A modified single solution method for the determination of phosphorus in natural waters. Anal Chim Acta 27:31–36

New York State Department of Environmental Conservation (NYS DEC) (2012) Standard operating procedure: biology monitoring of surface waters in New York State, pp 208–12

Pace ML, Cole JJ, Carpenter SR, Kitchell JF (1999) Trophic cascades revealed in diverse ecosystems. Trends Ecol Evol 14:483–488

Patrick R, Reimer CW (1975) The diatoms of the United States, exclusive of Alaska and Hawaii, vol 2, pt 1 Monographs of the Academy of Natural Sciences of Philadelphia, v 13

Pite DP, Lane KA, Hermann AK, Spaulding SA, Finney BP (2009) Historical abundance and morphology of *Didymosphenia* species in Naknek Lake, Alaska. Acta Bot Croat 68:183–197

Reid BL, Hernandez KL, Frangopulos M, Bauer G, Lorca M, Kilroy C, Spaulding S (2012) The invasion of the freshwater diatom *Didymosphenia geminata* in Patagonia: prospects, strategies, and implications for biosecurity of invasive microorganisms in continental waters. Conserv Lett 5:432–440

Richardson DC, Kaplan LA, Newbold JD, Aufdenkampe AK (2009) Temporal dynamics of seston: a recurring nighttime peak and seasonal shifts in composition in a stream ecosystem. Limnol Oceanogr 54:344–354

Ritchie RJ (2008) Universal chlorophyll equations for estimating chlorophylls a, b, c, and d and total chlorophylls in natural assemblages of photosynthetic organisms using acetone, methanol, or ethanol solvents. Photosynthetica 46:115–126

Rost AL, Fritsen CH, Davis CJ (2011) Distribution of freshwater diatom *Didymosphenia geminata* in streams in the Sierra Nevada, USA, in relation to water chemistry and bedrock geology. Hydrobiologia 665:157–167

R Development Core Team (2009) R: A language and environment for statistical computing. R Foundation for Statistical Computing

Schweiger EW, Ashton IW, Muhlfeld CC, Jones LA, Bahls LL (2011) The distribution and abundance of a nuisance native alga, *Didymosphenia geminata*, in streams of Glacier National park: climate drivers and management implications. Park Sci 28:88–91

Shannon CE (1948) A mathematical theory of communication. Bell Syst Tech J 27(379–423):623–656

Simberloff D (2011) Native Invaders. In: Simberloff D, Rejmanek M (eds) Encyclopedia of Biological Invasions. University of California Press, Los Angeles

Spaulding S, Elwell L (2007) Increase in nuisance blooms and geographic expansion of the freshwater diatom *Didymosphenia geminata*: recommendations for response. Pages open file report 2007-1425. http://www.epa.gov/region2008/water/didymosphenia/. Viewed 2023 Jan 2013. United States Environmental Protection Agency Region 8, Denver

Strayer DL (2010) Alien species in fresh waters: ecological effects, interactions with other stressors, and prospects for the future. Freshw Biol 55:152–174

Strayer DL (2012) Eight questions about invasions and ecosystem functioning. Ecol Lett 15:1199–1210

Sundareshwar PV, Upadhayay S, Abessa M, Honomichl S, Berdanier B, Spaulding SA, Sandvik C, Trennepohl A (2011) *Didymosphenia geminata*: algal blooms in oligotrophic streams and rivers. Geophys Res Lett 38:L10405

Turnipseed DP, Sauer VB (2010) Discharge measurements at gaging stations. U.S. Geological Survey Techniques and Methods book 3, chap A8, pp 1–87

Whitton BA, Ellwood NTW, Kawecka B (2009) Biology of the freshwater diatom *Didymosphenia*: a review. Hydrobiologia 630:1–37

Woolman L (1894) A report on the artesian wells in southern New Jersey. annual report of the State geologists. N J Geol Surv, Trenton