ABSTRACT

Ecosystem managers have often considered the nuisance diatom species, Didymosphenia geminata (didymo) as being introduced to the natural environment through human activities; however, observations from early 20th-century surveys challenge this characterization. We use diatoms preserved in lake sediment cores to investigate the history of didymo blooms from Gaspésie, Quebec. Relative abundances of diatoms were examined from the dated sediments of Lac Humqui and Lac au Saumon (a lake with an inflowing river currently supporting blooms). Didymo was observed throughout the Lac au Saumon core, demonstrating that it has been present in the region well before the first reports of blooms in 2006. Lac Humqui diatom assemblages experienced a shift in composition with declines in benthic taxa (attached to substrates) and increases in planktonic (free floating) diatoms that began ~1970. Strong relationships between this diatom shift, and increases in regional air temperatures and earlier river ice-out dates were consistent with the expected effects of climate warming on aquatic systems. Our paleolimnological evidence shows that climate warming, rather than human introduction, likely plays an important role in triggering didymo blooms.

KEY WORDS

Paleolimnology; Climate Change; Freshwater; Diatoms; Rivers

INTRODUCTION

Algal blooms of “rock snot” (Figure 1) were first reported as a nuisance species in rivers from eastern Canada in 2006.1 Blooms are a concern in Gaspésie (Quebec) and northern New Brunswick, and other regions, as blooms can potentially threaten highly-valued Atlantic salmon populations. “Rock snot” is the common name for a colonial diatom classified as Didymosphenia geminata (hereafter “didymo”), which is often found in North American and European rivers. It can form extensive mats several centimeters thick (referred to as blooms) on the bottoms of unshaded stretches of rivers or streams with stable flow patterns and often low nutrient concentrations.3,4,5 Blooms can alter the river bottom, with implications for many organisms.1,6,7 Many government agencies currently recognize didymo as an introduced species with the ability to affect the structure and function of river ecosystems.8 In North America, this has resulted in bans on felt-soled waders used by anglers, public awareness campaigns, and equipment-cleaning protocols to limit the spread of didymo.

Diatoms are a type of microscopic golden brown algae that have highly ornamented, glassy cell walls (valves) that are well preserved in sediments. Each species has its own environmental preferences, thus the
diatom assemblage (the collection of species) is highly reflective of its surrounding environment. "Introduced" or "invasive" are problematic designations for microorganisms such as diatoms, including didymo. It has been suggested that random dispersal (i.e. they have no barriers to spread from region to region) drives the distribution of diatom species. Thus, the idea of an invasive diatom species is difficult to confirm, as absence of evidence is not evidence of absence. Additionally, it is difficult to establish whether a species is truly absent using conventional sampling methods that may underestimate the presence of rare taxa. Therefore, determining whether didymo (and other diatom species) can truly be considered "introduced" is challenging. However, there is some evidence in reports written by diatomists from the early 20th century who observed this species throughout southern Quebec and New Brunswick, suggesting that didymo may indeed be native to the region.

The impacts of global climate change on recently reported blooms of didymo in the Gaspésie (as well as other regions) are poorly understood, but are suspected as a potential driver of blooms. Didymo blooms may become more frequent under warming conditions because of its ecological optima and tolerances; however, without long-term monitoring data it is difficult to determine whether the recently observed didymo proliferation is extraordinary in the context of the last ~100 years. Paleolimnology examines the physical, chemical and biological remains that are preserved in sediments that accumulate in lake basins and can establish what natural conditions were before, during, and after the onset of human activities ~150 years ago. By investigating the diatom taxa that lived in the lake over the past few hundred years and inferring the environmental conditions the assemblages reflect, we can produce important insights into the triggers of didymo blooms.

Our study, which was recently published with full scientific details and is summarized again here, examined diatom assemblage changes over time in dated sediment cores from two lakes in the Gaspésie region. Lac Humqui (LH), a “control” lake with no connection to rivers with didymo, and Lac au Saumon (LAS), an “impacted” lake with inflowing rivers affected by didymo were analysed to: (1) determine the history of didymo at the “impacted” site, thereby assessing claims that didymo is an introduced species, and (2) examine diatom assemblage changes at the “control” site to provide insights into possible mechanisms triggering recent proliferations of didymo in the study region. We hypothesized that didymo was not recently introduced to eastern Canadian rivers and that blooms were caused by environmental changes related to climate warming.

METHODS
Study lakes, sediment retrieval, and chronology
The “control” site (LH) is a headwater lake to the Humqui River in Gaspésie, Quebec, with one outflowing river (Humqui River that flows into the Matapedia River) where didymo blooms have been observed since 2006. The “impact” site (LAS) is a lake located ~30 km east of LH. The Matapedia River acts as both an inflowing and outflowing river of LAS and blooms occurring up to 56 km from the river’s mouth have been reported in the Matapedia River since 2006. Sediment cores from the
“control” lake (LH) and the “impacted” lake (LAS) were retrieved from the deepest basins through the ice in early March 2012 using a gravity corer and sectioned at contiguous intervals (Figure 2).

**Dating the lake sediment cores**

210Pb is a naturally occurring radioactive element with a half-life of 22.3 years. In order to use 210Pb to date lake sediments, we assume that lakes are receiving a constant input of atmospheric 210Pb. Given the half-life of 210Pb, we can determine that sediments deposited 22.3 years ago will be half as radioactive as those deposited yesterday. Standard radiometric techniques using 210Pb activities are sensitive enough to assign dates to sediments deposited in the past ~150 years. Many cores also exhibit a peak in 137Cs activity in recent sediments. 137Cs is an anthropogenic produced radioactive element that is released into the atmosphere during the detonation of nuclear bombs. In 1963, a worldwide moratorium was placed on intensive nuclear weapons testing, resulting in an increase and subsequent dramatic drop in 137Cs deposition. By comparing the location of this peak in the sediment core with the inferred 210Pb date, 137Cs can be used to support the accuracy of the 210Pb-inferred chronology.

When sediment deposition is high (e.g. in a riverine-like system such as LAS), 210Pb techniques may not be sensitive enough to assign accurate dates. In this case, “stable” Pb concentrations can be used to infer the approximate age of the sediments. Stable Pb was once a common element in gasoline, however atmospheric deposition has decreased as North America has tightened regulations surrounding leaded fuels and petroleum products. In order to establish an approximate age for the basal sediments of the LAS core, stable Pb was measured from 12 sediment intervals at LAS using standardized US EPA methods.

**Diatom processing from the sediment core**

For each sediment interval, microscope slides of diatom samples were processed from approximately 0.02 g of freeze-dried sediment following standard procedures. Approximately 400 diatom valves were identified and counted from each interval using a light microscope at 1000X magnification. Diatom counts were expressed as a percent relative abundance of the total number of valves counted. In ecological studies, relative abundances are a reliable measure of assemblage changes in space and time.

Conventional diatom counting methods (as described above) will underestimate the presence of large, rare species such as didymo. To better capture the historical trend in didymo, we counted all didymo valves encountered in an entire sediment sample for 20 intervals in our LAS sediment core. To do this, approximately 0.4-1.0 g of freeze-dried sediment was re-hydrated, warmed, and then sieved using a 38-μm mesh. Each sieved sample was then examined under a dissecting microscope at 35X magnification in sorting trays. All didymo
valves were counted and expressed as a concentration.

**Statistical analyses**
A temperature record from the Mont-Joli climate station (~80 km from the study lakes) extending to 1875 was obtained from the National Climate Data and Information Archive and a historical ice-off date record from 1894 to present was available for the Restigouche River near Matapédia. These measured climate data (temperature and ice-off date) were compared to changes in the relative abundances of certain diatom species (Cyclotella/Discostella) from the LH sediment core during this same period, using Pearson correlation methods. This type of analysis measures the strength of the linear relationship between two variables.

**RESULTS**

**Lake sediment dates**
The LH sediment core exhibited an exponential 210Pb decay curve and a well-defined 137Cs peak suggesting that sediment mixing was not an issue. After applying the Constant Rate of Supply (CRS) model to infer sediment ages, the 15-cm interval was estimated at ~1864. A 137Cs peak (associated with fallout from nuclear bomb testing decades ago) at the 8-cm interval supports the estimated 210Pb date of ~1965 at that same interval.

In the LAS core, the low activities and the lack of an exponential decay in 210Pb concentrations suggested that estimating ages as described above is not possible. This is not entirely unexpected, given the riverine-like depositional basin cored. Using the stable Pb profile, we estimate an age of ~1970 for the LAS basal sediments, but cannot assign precise ages to the sediments between the basal (~1970) and uppermost (2012) core intervals.

**Didymo concentration data from Lac au Saumon**
Didymo was observed throughout the LAS core in 19 of 20 sediment intervals (Figure 3). Between the base of the core (41 cm, or ~1970) and the 10 cm depth, an average of 9 didymo valves per interval were observed (min = 0, max = 26), with an average concentration of

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**Figure 3** Concentration of didymo valves (# valves/g dry wt.) from the Lac au Saumon core. The inset shows a photomicrograph of a didymo frustule found at the 2 cm interval. Photo by J. Michelle Lavery. The open circle represents no didymo observed. Modified from Lavery et al. (2014).

**Figure 4** Relative abundances of the most common diatoms in the Lac Humqui (“control” lake) core. Diatom taxa were grouped into genera for clarity. The onset of increased temperatures and official reports of didymo in the region are indicated with grey bars. Ages are shown to the left of the y-axis. Photos top (left to right: Cyclotella stelligera and C. comensis). Photos bottom (left to right: Fragilaria construens var. venter and F. construens). Photos by Kathleen M. Rühland. Originally published in more detail in Lavery et al. (2014).
48 valves/g of dry sediment. At 8 cm, didymo increased to 1300 valves/g of dry sediment. Between 8 cm and modern times, concentrations increased further, averaging 10580 valves/g of dry sediment. Peak concentration of 24,850 valves/g of dry sediment occurred at 4 cm with a total of 1548 valves counted from that interval. Compared to baseline concentrations (48 valves/g), the average concentration between 8 cm and 2012 has increased by ~200 times.

**Diatom assemblage trends from Lac Humqui**
The LH core contained a total of 85 diatom species, many of which occurred in low relative abundances. Several diatom species dominated the LH core, including, benthic fragilarioid taxa and planktonic diatoms (small Cyclotella/Discostella taxa) (Figure 4). The most noticeable shift in the diatom assemblages was an increase in the relative abundances of planktonic taxa, including small Cyclotella/Discostella species (from ~1% to 30%) and Asterionella formosa (~1% to ~10%) starting ~1970, with the former reaching average modern abundances (~24%) by ~1990. Over this same time period, benthic fragilarioid taxa decreased (~60% to ~30%).

**Air temperature and ice-off correlations**
Mean annual air temperature data from Mont-Joli showed a warming of 3.4°C over the 133-year record (Figure 5A). This warming trend was observed in all seasons, although winter showed the greatest temperature increase. Beginning in the 1980s, the annual temperatures recorded were consistently the highest throughout the entire record, especially those after ~2000 (Figure 5A). Mean annual temperatures were positively correlated with planktonic Cyclotella/Discostella taxa (r = 0.72, P<0.001) (Figure 5B). A relatively complete (~1890-1998) record of Restigouche River ice-off dates near Matapédia showed that modern (~1995) ice-off is occurring ~9 days earlier in the spring than during the early 1900s (Figure 5C). Ice-off day of the year was negatively correlated with increasing planktonic Cyclotella/Discostella taxa (r = -0.63, P<0.01) (Figure 5D).

**DISCUSSION**
The historical occurrence of didymo in Gaspésie
Paleolimnological studies have rarely been used to determine if a species is “introduced”, yet these approaches often offer the only sources of generating such data. The occurrence of didymo throughout the sediment record at LAS (Figure 3), in combination with direct observations from early 20th-century diatom surveys, refute claims that didymo is an introduced species to eastern Canada. The first official accounts of didymo blooms in the region were reported in 2006, post-dating the occurrence of didymo in our sediment record by ~40 years. The low didymo concentrations noted in basal samples from the LAS core (Figure 3) clearly demonstrate that didymo has been a component of the regional river diatom assemblage since 1970, and possibly as early as the beginning of the 20th century. The presence of didymo throughout the sediment record, together with the 200-fold increase in didymo concentrations in the more recent sedimentary intervals in LAS, points to an environmental trigger rather than a recent “introduction” via human transfer to Gaspésie rivers. Although we were only able to assign an approximate date to the didymo rise in the LAS record using stable Pb techniques, it is likely coincident with the warmest mean annual temperatures and the earliest ice-off dates recorded in the last decade, as well as the highest abundances of planktonic diatoms in our control lake. Our data clearly show that “invasion” or transfer to the Gaspésie region is an unlikely explanation for current didymo blooms.

Lake responses to climate change in Gaspésie
Diatom assemblage shifts at LH are evidence of significant changes in the aquatic environment (Figure 4). Strong relationships between our diatom data at LH and observed temperature and ice-off records (Figure 5) demonstrate that freshwater systems in Gaspésie are responding to recent climate warming. The pronounced shift from an assemblage dominated by benthic fragilarioid taxa in the older sediments at LH, to an abrupt increase in small, planktonic Cyclotella/Discostella species in recent decades
(Figure 4), has been observed throughout the northern hemisphere, including >150 lakes in temperate regions, that were minimally affected by human activities. This species-specific shift has since been established as a predictable assemblage response to recent climatic warming and the associated changes to aquatic environments. Small, planktonic diatoms (e.g. Cyclotella and Asterionella taxa) have a high surface area to volume ratio, and therefore have a relatively low sinking rate, which gives them a competitive advantage by remaining buoyant in the water column longer. Warmer conditions with less ice cover and longer growing seasons tend to favor open-water, planktonic diatoms, particularly if thermal stratification is strengthened and water column mixing is reduced. Conversely, small benthic fragilariid taxa tend to be more competitive during cooler periods with extended ice cover as these opportunistic and pioneering species are often able to proliferate beneath the lake ice.

Figure 5 (A) Mean annual air temperature from the Mont-Joli climate station, (B) Pearson correlation between harmonized temperature data and small planktonic Cyclotella taxa, (C) Historic observations of Restigouche River ice-off day of year near Matapédia, and (D) Pearson correlation between harmonized ice-off data and small planktonic Cyclotella taxa. Originally published in more detail in Lavery et al. (2014).

Didymo: a sentinel of climate-induced change in Gaspésie river ecosystems

The exceptional rise in didymo abundance from low, stable levels to ~200 times above baseline concentrations in the LAS core (Figure 5) suggests that there has been an ecologically significant shift in the aquatic environment towards conditions that favour didymo blooms. Didymo generally prefers low-nutrient riverine sites with low mean discharge and stable stream flows, since flashy, high flows tend to scour blooms from the river bottom and alter water chemistry and light regimes. Recent warming is known to reduce the extent and duration of lake and river ice, including its seasonality, and also cause shifts in both the timing and intensity of disturbance regimes (flow, ice scour, river bed movement) of rivers and streams. An earlier ice-off and longer open-water period may begin to set the stage for changes in season river conditions (e.g. stable base flow, lower nutrients, and clearer waters) that are advantageous to the formation...
of didymo blooms. This is especially true in rivers that experience declines in nutrient inputs from the catchment as a result of, or in combination with, climate-induced environmental change.\textsuperscript{13,30} Given didymo’s known habitat and environmental preferences, together with our evidence for changes in diatom assemblage composition in response to recent warming, our results suggest that climate-related changes in regional rivers are likely an important factor that favours didymo’s recent proliferation in the Gaspésie, and possibly other regions.

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For more on paleolimnology by Dr. John Smol

For more on Michelle Lavery’s research
RESOURCES


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Q&A WITH THE AUTHOR

What is the most fulfilling aspect of working in your research field?

The most fulfilling moments in research happen quietly, in an office in the bowels of a university. They are the golden moments of discovery – where patterns are finally recognized and explained after years of hard work and frustration. They are what make it all worthwhile. That being said, when your research captures the attention of the general public, you know you’re making a difference. This can be incredibly fulfilling, but it doesn’t happen often. We need more scientists with the ability to communicate their passion for science to the general public to ensure our golden moments of discovery don’t fade into obscurity.

What are the biggest challenges faced by your field of research today?

Environmental scientists face numerous challenges, from lack of funding to outright rejection of our conclusions by the public and policy-makers. We must be researchers, scientists, advocates, and effective communicators – all at the same time. Oftentimes, our extensive education does not include sufficient communication training and development, which hinders our ability to collaborate and promote our work. Without the ability to garner support from the general public, we often lose out on important funding opportunities and our results are rejected out of confusion and misunderstanding.

In what direction do you see your field moving?

I think that all fields of science are, and should be, moving towards interdisciplinary research. We cannot sustain a culture of segregated “departments” any longer if we wish to produce meaningful, helpful results. Scientists from all corners of the world must work together, instead of straining in opposite and obscure directions. PEARL is a good example of such an environment in which biologists, chemists, geologists, etc work as a team to find answers in the limnological record. This kind of collaboration can provide insights from multiple perspectives and deepen the conclusions of the research, adding meaning and enhancing understanding.

What advice would you give to high school and undergraduate students interested in environmental research?

I would highly suggest improving your communication skills as much as possible by taking advantage of university writing centres, friendly English professors, and mentors. We don’t have enough scientists with the ability to effectively communicate their results to a general audience. Without the public’s support, we will fade into obscurity and lose funding for our research.

Additionally, I strongly suggest diversifying your undergraduate courses. A well-rounded scientist is able to examine a problem from multiple perspectives, which reduces bias and enhances understanding. A sociology or gender studies course will help you understand your future colleagues and the world around you.

Finally, get practical experience! Volunteer with a professor you find interesting, apply for summer research positions, or take a field course. These will be handy both on your resume and when it comes time to do real fieldwork. Don’t be afraid to get dirty either – take a survival course and test your limits in nature. These experiences will provide you with invaluable knowledge when you’re in charge of a research team. Alternatively, these experiences will indicate that you are not suited for fieldwork, which is equally invaluable knowledge.