# The Origin of Invasive Microorganisms Matters for Science, Policy, and Management: The Case of *Didymosphenia geminata*

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*The value of distinguishing native from nonnative invasive species has recently been questioned. However, this dichotomy is important for understanding whether a species' successful dominance is caused by introductions, changing environmental conditions that facilitate an existing population, or both processes. We highlight the importance of knowing the origin of hard-to-detect invasive microorganisms for scientific research, management, and policy using a case study of recent algal blooms of the stalk-producing diatom* Didymosphenia geminata. *Nuisance blooms have been reported in rivers worldwide and have been hastily attributed to introductions. However, evidence indicates that blooms are probably not caused by introductions but, rather, by environmental conditions that promote excessive stalk production by this historically rare species. Effective responses to invasive microorganisms depend on knowing whether their proliferation is caused by being nonnative or is the result of changing environmental conditions that promote invasive characteristics of native species.*

*Keywords: algal blooms, diatom, environmental change, phosphorus, exopolymers*

**Policy and management responses to invasive** species are contentious (e.g., Davis et al. 2011, but see Simberloff et al. 2012). Recent controversy stems from whether distinguishing native from nonnative invasive species is useful or whether responses to invasive species should be focused on the benefits or harm that result. Calls for the end of invasion biology as a field of study claim that the distinction between native and nonnative invasive species has limited practical value (e.g., Valéry et al. 2013). However, knowing whether a species exhibiting invasive characteristics is native or nonnative can be essential for understanding the mechanisms behind its recent success (Simberloff et al. 2012). Correctly identifying an invasive species as either native or nonnative is important for developing sound policy, management, and scientific research programs, because effective responses depend on knowing whether the species' dominance is caused by ecological or evolutionary novelty, changes in environmental conditions that facilitate it, or both processes. Given increasingly limited resources, policy and management should be focused on those species with the potential to cause the greatest degree of environmental harm (Davis et al. 2011); however, this criterion, by itself, does not provide insight into how to control a species' invasiveness or impact. Rare or hard-to-detect microorganisms may also be an important exception to the idea that a species' impact is more important than its origin. Establishing the origin of a microorganism exhibiting invasive characteristics seems paramount to determining whether policy and management should target the initial dispersal, establishment, spread, or the environmental conditions promoting the invasiveness.

The recent global occurrence of algal blooms in rivers by the diatom *Didymosphenia geminata* (Lyngbye) M. Schmidt provides an example of the problems associated with incorrectly labeling an invasive species as *nonnative* and the implications of this error for policy and management decisions. *Didymosphenia geminata* has generated widespread concern because of the possible impacts on the pristine rivers in which blooms primarily occur and the salmonid fisheries that these rivers often support. *Didymosphenia geminata* blooms result from excessive extracellular stalk production by individual cells that eventually coalesce to form a contiguous mat covering the stream bottom (figure 1). Claims that the recent blooms are caused by either a novel stalk-producing genotype or a single genotype rapidly introduced worldwide

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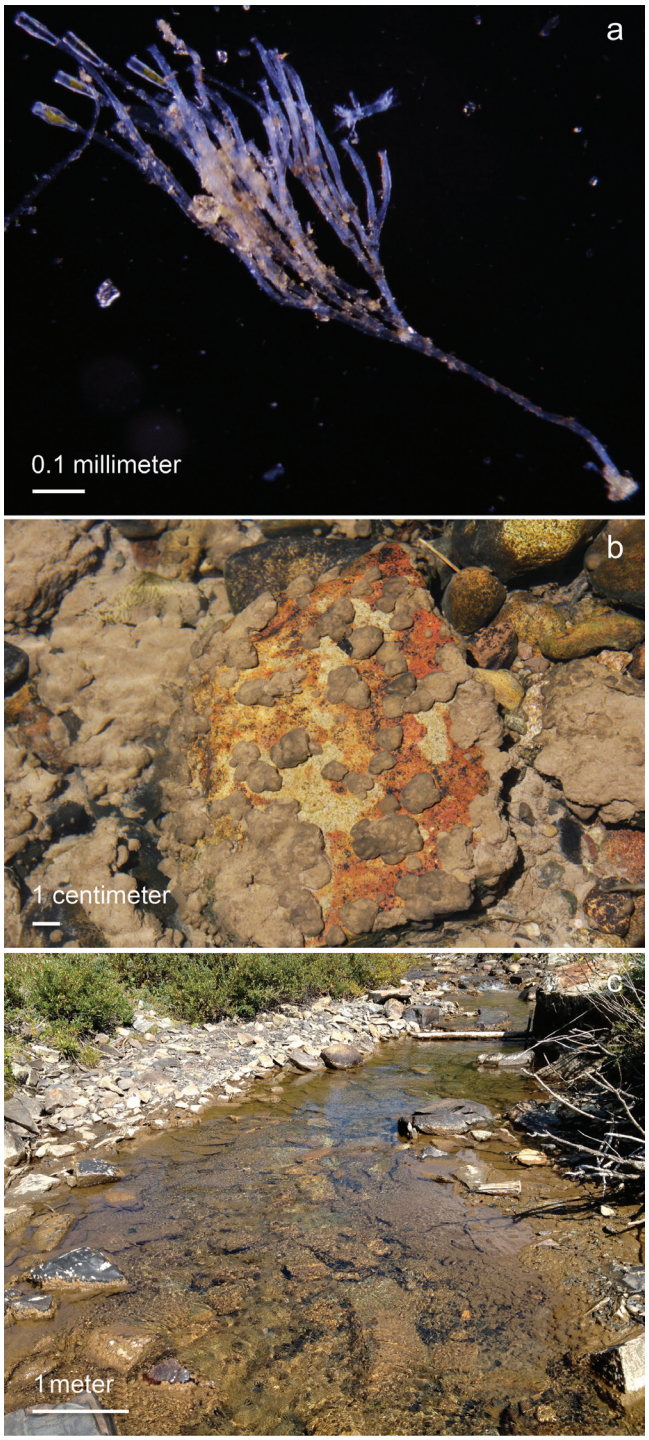



***Figure 1.*** **Didymosphenia geminata** ***(a) cell and extracellular stalk produced from one cell and its subsequent asexual reproduction that is apparent at each branching event, (b) colonies forming tufts on the stream bottom, and (c) mats (the tan-colored areas) covering large areas of Oh-Be-Joyful Creek, in the Rocky Mountains near Crested Butte, Colorado. Photographs: Brad W. Taylor.***

have been widely publicized and readily accepted (e.g., Segura 2011). However, few data support these claims. Nevertheless, the premise that blooms are caused simply by new introductions has led to recent legislation and appropriation of resources into the millions of US dollars to control *D. geminata* introductions by several states in the United States and the governments of New Zealand and Chile. However, prematurely declaring a species with invasive characteristics as a newly introduced nonnative can lead to poor decisions about its management by diverting funding to programs that may be futile and that may thwart efforts to understand the true cause of the invasiveness. We contend that current evidence does not support the conclusion that all contemporary *D. geminata* blooms are caused simply by new introductions.

## Are blooms caused by introductions to new areas?

We can dismiss the notion that the recent global occurrence of *D. geminata* blooms are caused solely by cells' being introduced, because similar, nearly synchronous blooms occur in areas where its native status has been unquestioned for hundreds of years. Fossil and historical collections place *D. geminata* in the same watersheds where blooms occur today (table 1). Moreover, fossil and historical records place *D. geminata* on all continents except Africa, Antarctica, and Australia; records place *D. geminata* in Asia (China, India, Japan, Mongolia, Russia), Europe (Denmark, Finland, France, Germany, Ireland, Italy, Norway, Poland, Portugal, United Kingdom, Sweden), and North America (Canada and the United States), and historical records dating back to the 1960s place *D. geminata* in South America (Chile; Blanco and Ector 2009, Whitton et al. 2009). The recent blooms of *D. geminata* are found on each of these continents, where fossil or historical records have been documented, which indicates that attributing all blooms to recent introductions or to range expansion is incorrect. However, this fossil and historical information has been ignored, and the idea that *D. geminata* is a recently introduced species or a native species expanding its range has been accepted and promoted (e.g., Segura 2011). In fact, citing the threat of human-induced translocations of *D. geminata* or other unwanted organisms, seven US states (Alaska, Maryland, Missouri, Nebraska, Rhode Island, South Dakota, and Vermont), Chile, and New Zealand have passed legislation banning the use of felt-soled waders and boots in inland waters (e.g., the 1993 New Zealand Biosecurity Act, Chile's law no. 20.254, Vermont 2013 Act no. 130 [H.488]). Although such restrictions may reduce introductions of other deleterious aquatic microorganisms, the connection to the spread of *D. geminata* within its native range seems dubious. Clearly, *D. geminata* is not a recently introduced species to these regions (table 1).

Furthermore, the occurrence of blooms has been equated with the notion that *D. geminata* is a nonnative invasive, which is incorrect; some native organisms can be highly productive and invasive (Simberloff et al. 2012). Moreover, *D. geminata* does not bloom in all rivers where its cells are present. For example, in some New Zealand rivers with *D. geminata* cells present, visible growths are rarely or never observed; therefore, the presence of cells does not always


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*Table 1. Locations of fossil or historical records of* **Didymosphenia geminata** *cells and contemporaneous* **D. geminata** *blooms.*

| Drainage basin | River or lake | Location | Year of historical or fossil record | Year of contemporary bloom | Reference |
|---|---|---|---|---|---|
| Delaware | Delaware River | New York and Pennsylvania | 10,000 years ago | 2007[a] | Boyer 1895 |
| Naknek | Brooks River | Alaska | 1200 | 2007 | Pite et al. 2009 |
| Coquet | Coquet River | United Kingdom | 1851 | 1950 | Whitton et al. 2009 |
| Tana | River Tana | Norway | 1868 | 1989 | Lindstrøm and Skulberg 2008 |
| Unknown | Unknown | Vancouver Island, British Columbia | 1894 | 1989 | Cleve (1893) 1965 |
| Drammenselva | River Drammenselva | Norway | 1911 | Semipersistent | Lindstrøm and Skulberg 2008 |
| St. Lawrence | Matapédia River | Quebec | 1915 | 2006[b] | Miller 1915 |
| Puntledge | Puntledge River | Vancouver Island, British Columbia | 1978 | 1991 | Munro et al. 1985, Bothwell et al. 2009 |
| Cisnes | Rio Cisnes | Aysen, Chile | 1963 | 2012[c] | Asprey et al. 1964, Rivera and Gebauer 1989 |
| Colorado | East River | Colorado | 1968 | 2006 | Livingston 1968 |
| Colorado | Gunnison River | Colorado | 1962 | 2006 | Reed and Norton 1962 |
| Unknown | Unknown | Virginia | 1975 | 2006[d] | Patrick and Reimer 1975 |

[a]*www.dec.ny.gov/animals/54244.html* and *www.fish.state.pa.us/water/habitat/ans/didymo/faq_didymo.htm*
[b]*www.mddep.gouv.qc.ca/eau/eco_aqua/didymo/didymo-en.pdf*
[c]*www.subpesca.cl/institucional/602/articles-80165_Resultados_Prospeccion_de_D__geminata_CentroSur__Carolina_Diaz.pdf*
[d]*www.dgif.virginia.gov/fishing/didymo.asp*

lead to blooms (Kilroy and Unwin 2011). Similarly, in the Colorado Rocky Mountains, *D. geminata* cells are present in numerous rivers and have been for at least 55 years, but blooms occur only in some rivers. The observation that *D. geminata* cells can be present without blooming is repeatable within individual rivers, as well. For example, blooms in the Batten Kill River occurred in downstream sections in New York but not in upstream sections in Vermont; however, cells are present in both sections (Matthews et al. 2008). A similar longitudinal distribution of *D. geminata* cells and blooms has been observed in Canadian rivers (Kirkwood et al. 2007). These results are inconsistent with blooms' being caused solely by introductions of *D. geminata* and are more consistent with well-known highly plastic responses of photoautotrophs to environmental conditions. In the case of *D. geminata*, increased stalk production is the growth form that characterizes blooms.

The assertion that the recent blooms are caused by inadvertent introductions of *D. geminata* cells by humans comes from frequent reports of blooms in areas that are used for recreation or monitoring by various agencies (Bothwell et al. 2009). Although Kilroy and Unwin (2011) reported a correlation between the ease of river access and *D. geminata* blooms in New Zealand, this has not been found in North American studies. In fact, systematic observations at both rivers with frequent human activities and remote rivers not heavily used for recreation or monitoring reveal no association between human activities at a river and blooms in Glacier National Park, in Montana (Schweiger et al. 2011). Moreover, pathways for introducing *D. geminata* cells have existed for decades (e.g., felt-soled shoes; the transport of fish, their eggs, and water from areas where *D. geminata* is determined to be native on the basis of fossil records), making inadvertent introductions by humans difficult to explain, given the recent worldwide synchrony of blooms. Although an alternative explanation is a long time lag between the initial introduction and the ability of *D. geminata* to produce blooms, this does not explain the bloom phenomena in areas were *D. geminata* has been native for several centuries.

## Fossil evidence

Classifying an invasive species as *nonnative* relies on its not being observed at a locale over millennia. In the case of rare or hard-to-detect microorganisms such as *D. geminata*, differentiating between true absence and inadequate sampling can be problematic. For example, the lack of *D. geminata* cells in lake sediment cores has been used to support its absence from locations over millennial timescales. However, inference about the absence of a primarily stream-dwelling species from locations on the basis of lake cores depends on several factors. Foremost, the cores must come from lakes whose position in the watershed is below rivers suitable for *D. geminata*, and the cores within a lake must come from areas near fluvial inflows, because the cells sink rapidly. Nonetheless, fossil collections place *D. geminata* in the Arctic, Asia, Europe, and North America from the period of last glaciation (10,000 years ago), but fossil evidence is needed from other continents (e.g., South America) and


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New Zealand to more clearly establish the historical presence of *D. geminata* in various regions.

The effort required to detect a rare diatom taxon in sediment cores is seldom put forth, which may lead to erroneous conclusions about the diatom's absence. An example that may be analogous to *D. geminata* blooms comes from the lake diatom *Stephanodiscus binderanus*, which was initially identified as a nonnative invasive introduced to the Great Lakes from Eurasia; however, recent lake core data show that this species was present in nearby (less than 50 kilometers away) Lake Simcoe since at least the seventeenth century (Hawryshyn et al. 2012). The recent increase in abundance of this species in the Great Lakes has been attributed to changing environmental conditions—namely, eutrophication—which makes it appear to have been recently introduced. For many rare diatom species, additional intensive sampling will likely show that they have a wide geographical distribution (Finlay et al. 2002). Therefore, the argument for the endemism of *D. geminata* or other rare diatoms is untenable, because it is impossible to disprove their presence elsewhere using current sampling methods (Hawryshyn et al. 2012).

Fossil evidence is important for establishing the historical presence of hard-to-detect species. This is especially true for diatoms that have resting stages that are morphologically difficult to identify, which enables the species to reside undetected but with the capacity to increase in abundance when environmental conditions are favorable. Even in rivers where *D. geminata*'s native status is unquestioned in the Colorado Rocky Mountains, its relative abundance can be so low (less than 1%) that it is either not reported as an individual taxon in many publications or is mentioned only briefly. Similarly, in British Columbia, during the late 1970s, *D. geminata* was present in the Puntledge River, on Vancouver Island, but was not sufficiently abundant to make the list of quantifiable taxa (Munro et al. 1985). In an extreme case, the difficulty in detecting *D. geminata* resulted in its listing as an *endangered* species in a German red list of diatoms (Whitton et al. 2009). Together, this evidence indicates that introductions of *D. geminata* cells to new areas cannot solely explain the recent bloom phenomena by this diatom.

## Are blooms caused by the emergence and spread of novel stalk-producing genotypes?

Molecular phylogeographic data are lacking for most freshwater diatoms, and *D. geminata* is no exception. However, in two recent studies, *D. geminata*–specific primers have been used to amplify the internal transcribed spacer (ITS) region to investigate the phylogeographic relationships of bloom-forming populations. On the basis of cloned ITS, the data in Kelly (2009) suggest that populations in North America, Europe, and New Zealand may have experienced high reciprocal gene flow, but it is not possible to determine either the time frame or the direction in which these exchanges occurred. However, a study within North America found high intragenomic variation, which suggests that ITS may not be suitable for fine-grain phylogeographic studies of *D. geminata* (Teofil Nakov, University of Texas, Austin, Texas, personal communication, 11 November 2013). The data thus far do not preclude the possibility of a large panmictic *D. geminata* population, but they also do not preclude the possibility that *D. geminata* is highly structured but that ITS fails to capture the structure. Many freshwater and marine diatom species have a cosmopolitan distribution that was determined on the basis of morphological species classification, and molecular analyses have revealed both low and high degrees of spatial genetic differentiation within diatom species (Vanormelingen et al. 2008). Any future molecular analyses should move beyond the ITS region and should consider sampling not only bloom populations but also nonbloom populations. Taken together, the molecular analyses thus far have been inclusive in identifying whether *D. geminata* blooms are caused by the emergence and introduction of novel stalk-producing genotypes, and fossil collections provide greater evidence of the global historical distribution of *D. geminata* cells.

Although genomic studies have thus far failed to provide convincing phylogeographic relationships, observations of the spatial and temporal characteristics of blooms strongly indicate that the emergence of novel stalk-producing genotypes or a single stalk-producing genotype is not involved in the global spread of blooms. First, blooms of *D. geminata* are not new phenomena; they occurred hundreds of years ago within its native range and were transient events (e.g., in Europe; Lindstrøm and Skulberg 2008, Blanco and Ector 2009), which is not consistent with a novel genotype causing the recent blooms in these areas. Second, adjacent streams can all have *D. geminata* cells, but blooms form only in some streams. Streams with and without blooms can be in closer spatial proximity to each other than are streams with blooms, which is not consistent with blooms caused by the spread of a stalk-producing genotype. Nonblooming populations of *D. geminata* are also present in multiple rivers in New Zealand (Kilroy and Unwin 2011, Kilroy and Bothwell 2012), which is not consistent with the idea that blooms are caused by recent introductions of a bloom-forming genotype. Third, live *D. geminata* cells are found along the lengths of some streams, but blooms often develop in the middle sections of rivers (Kirkwood et al. 2007, Kilroy and Unwin 2011), and subsequent blooms typically occur upstream and not downstream, which is not consistent with blooms caused by introductions of stalk-producing genotypes, given the massive downstream movement of *D. geminata* cells. Fourth, the development of blooms is environmentally dependent on dissolved phosphorus (P) concentrations (Kilroy and Bothwell 2011, 2012). Experiments in which the same genotypes of *D. geminata* were used have shown that two phenotypes—bloom and nonbloom—can be produced, depending on the amount of dissolved P in the water (Kilroy and Bothwell 2011, 2012). Likewise, there are anecdotal observations of blooms disappearing below municipal nutrient outfalls and the initiation of large, recurring blooms in the Kootenai River, Montana, followed the


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cessation of P loading because of the closure of the Sullivan Mine in 2001 in British Columbia. Furthermore, experimental translocations of *D. geminata*–covered substrata to multiple rivers without blooms revealed rapid declines in *D. geminata* cell viability and biomass compared with the substrata in rivers with blooms (Sutherland et al. 2007), which suggests that specific environmental conditions are needed to induce and sustain stalk production. Taken together, the P addition and reciprocal transplant experiments indicate that the same genotype can give rise to two different phenotypes, bloom and nonbloom *D. geminata*. Therefore, the emergence and spread of novel genotypes or a single stalk-producing genotype is not necessary, nor is it the most parsimonious explanation for the recent blooms. Although there is the possibility of a genotype × environment interaction as a cause of the blooms, this seems unlikely, because it requires either the same mutation to have occurred in rivers with blooms around the world or the global spread of a stalk-producing genotype combined with an environmental change. The global spread of a stalk-producing genotype hypothesis also raises the conundrum of where the new genotype or genotypes originated, especially for areas where blooms occurred in the past. Therefore, novel stalk-producing genotypes or a single genotype that has been introduced around the world are unlikely explanations for the recent blooms, because these depend on numerous assumptions that are not supported by data or the natural history of *D. geminata*.

## Are the recent blooms caused by changing environmental conditions?

Species composition and the relative abundance of diatom taxa have been used as indicators of river water quality and, therefore, of changing environmental conditions (e.g., nutrients) in rivers and lakes for many decades. Chief among these conditions is that specific diatom taxa reflect the P concentration of the water that they inhabit (Stevenson et al. 2008). The emergence of a novel genotype was initially offered as an explanation for the blooms, because no known environmental changes preceded their onset (Bothwell et al. 2009). However, research has now shown that blooms occur only in rivers with very low dissolved P concentrations, near or below the detection limit of most analytical methods (Kilroy and Bothwell 2012, Bothwell et al. 2014); therefore, no clear signal would be present in many existing water chemistry databases connecting *D. geminata* blooms to this environmental change. Extracellular stalk production in response to extremely low P may be a strategy by this diatom to extend cells out of the benthic boundary layer and into the water column, where there is greater delivery of growth-limiting P. The release of extracellular photosynthate by diatoms is not unusual under nutrient-limited conditions (e.g., Hoagland et al. 1993). Stalk production in response to nutrient limitation has been observed in other freshwater benthic diatoms (e.g., Stelzer and Lamberti 2001), but the magnitude of the response in terms of the stalk biomass produced by *D. geminata* is unprecedented (e.g., 3 kilograms dry mass per square meter). The enormous response by *D. geminata* to low P could be linked to this large diatom's low surface-area-to-volume ratio relative to those of other stalk-producing diatoms and, therefore, a lower threshold to changes in P. A similar stalk-producing morphological response to P limitation has also been reported for the bacterium *Caulobacter* (Gonin et al. 2000), so the response may be general across diverse groups of benthic organisms.

Environmental change can facilitate the establishment and spread of nonnative species, but it is not always a prerequisite (Simberloff et al. 2012). Changes in environmental conditions facilitating introductions do not explain the recent *D. geminata* blooms in areas where it is confirmed native, however. Although there is limited evidence that *D. geminata* was present in New Zealand prior to 2004 (Kilroy and Unwin 2011), the current distribution of *D. geminata* blooms has an inverse correlation with dissolved P in the rivers on the South Island. Moreover, its absence from North Island rivers with naturally higher P and similar fishing pressure indicates that more is involved in the establishment of blooms than simply the introduction of cells, even in New Zealand (Kilroy and Bothwell 2012).

Alternative explanations for the recent blooms based on drought-induced reductions in disturbance are not supported by data (Sherbot and Bothwell 1993) or occurrences of blooms in nondrought areas (e.g., rivers in northeastern United States). Likewise, there is little evidence to suggest that the recent worldwide blooms are a long-term cyclic phenomenon, because centuries-old writings by the scientific and angling communities rarely mention blooms (although accounts of blooms in Scandinavian rivers date back a hundred years; Lindstrøm and Skulberg 2008) and because the data from lake cores do not show peaks in *D. geminata*'s relative abundance that would be missed by contemporary limnology (e.g., Pite et al. 2009). The only consistent environmental factor linked to bloom development is low P.

## What are the possible causes of declines in phosphorus?

Many recent blooms have occurred in remote rivers that have been subject to relatively little historical human impact. The recent and nearly simultaneous appearance of blooms in geographically distant areas of the world (North America, New Zealand, and Chile) implies a common explanatory factor for blooms in suspected new areas and where *D. geminata* has occurred for decades. Global changes that are decreasing P may be the ultimate causes of recent blooms. There are several potential mechanisms that may be decreasing dissolved P in rivers with blooms. For example, atmospheric nitrogen (N) deposition has shifted algae from being N limited to being P limited in lakes and rivers (Hessen 2013). The possibility that N deposition is shifting rivers toward P limitation warrants further investigation. In addition, climate-induced shifts in the timing of springtime snowmelt and runoff are affecting rivers with blooms worldwide (Stewart et al. 2005, Hodgkins and Dudley 2006, Lundquist


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et al. 2009) and constitute another likely mechanism that can decrease P. Hydrologic shifts can cause earlier, more-abrupt spring pulses in nutrients, which result in lower concentrations during the summer growing season (Williams et al. 1996, Corriveau et al. 2011). This trend toward an earlier growing season and soil thawing can also increase nutrient uptake by soil microbes, terrestrial plants, and microbes in lakes upstream, thereby decreasing nutrients to rivers (Bernal et al. 2012). In addition, the trend toward earlier snowmelt and declining snowpack results in decreased cloud cover and, therefore, in greater inputs of photosynthetically active radiation during late spring and early summer, which, combined with reductions in P, creates ideal conditions for rapid stalk production by *D. geminata*, according to experimental manipulations of light (Kilroy and Bothwell 2011). Other factors may interact with the above global-scale processes to produce the local-scale spatial heterogeneity of blooms. For example, blooms are more common in rivers draining lakes and in rivers downstream of dams built by humans or beavers (Kirkwood et al. 2007, Spaulding and Elwell 2007). Lakes and dams can intensify declines in P in rivers downstream through increased uptake or removal of P from the water column as a result of sedimentation (Powers et al. 2014). Together or independently, these are plausible mechanisms that could reduce P in rivers and trigger the recent increase in *D. geminata* stalk production worldwide.

## Implications for current and future research, management, and policy

Current data indicate that the science, management, and policies related to *D. geminata* blooms should be redirected. Presently, most science, management, and policy is directed at preventing *D. geminata* introductions to control blooms. For example, the absence of *D. geminata* from North Island, New Zealand, has been widely attributed to the "Check, Clean, Dry" social-marketing campaign. However, the appearance of *D. geminata* blooms on South Island, New Zealand, is inconsistent with an introduction based on propagule pressure, because the North Island is the port of entry for 80% of international visitors. A more parsimonious explanation for the absence of *D. geminata* blooms on North Island is higher dissolved P concentrations in many North Island rivers, which drain predominantly young, P-rich volcanic bedrock, compared with lower dissolved P concentrations in South Island rivers, which drain a mix of older P-depleted metamorphic and sedimentary bedrock. In theory, decontamination programs are a first-line defense against the spread of unwanted organisms, but whether such programs can prevent or slow the spread of free-living microorganisms, in particular, is unclear. We know of no example in which a decontamination program has fully prevented the spread of a free-living microorganism. Even the strictest maritime quarantine on record did not prevent the spread of the H1N1 influenza virus of 1918 to many Pacific Islands. Therefore, we do not recommend investing research, management, and policy efforts into programs to specifically prevent *D. geminata* introductions or spread, regardless of whether it is native or nonnative. All of the evidence indicates that this approach simply does not work.

Moreover, current efforts to control blooms by whole-stream chemical poisoning of *D. geminata* can have greater ecological costs than benefits. For example, short-term (1-hour) but repeated (weekly) additions of a chelated copper solution—Gemex, developed and tested in New Zealand to poison *D. geminata*—caused significant localized trout mortality (Clearwater et al. 2011). The trout mortality was likely due to the low buffering capacity of the river, changes in chelated copper speciation, or both. Although the Gemex additions killed *D. geminata* cells, the stalks, the characteristic nuisance feature of this diatom's bloom, remained attached to the stream bottom for at least 3 weeks (Clearwater et al. 2011). Moreover, Gemex and other broad-spectrum toxins may adversely affect nontarget algae, thus disrupting the base of the food web. Synoptic surveys in New Zealand have shown that *D. geminata* blooms do not develop in rivers when concentrations of dissolved inorganic P exceed about 2 micrograms per liter over prolonged periods of time (Kilroy and Bothwell 2012), which suggests that P augmentation might be an alternative control for *D. geminata* blooms. Recently, this approach has been demonstrated to significantly reduce *D. geminata* bloom development, especially stalk production, in a short section of Rapid Creek, South Dakota (Daniel James, US Fish and Wildlife Service, Pierre, South Dakota, personal communication, 1 November 2013). However, P additions provide only a short-term control, because P must be applied continuously in order to prevent bloom development. Moreover, the idea of elevating P concentrations in low-nutrient rivers runs counter to widespread efforts aimed at reducing P inputs to prevent cultural eutrophication, especially in downstream lakes. For these reasons, as well as the cost and logistics of maintaining a continuous whole-stream P addition, this approach is not advisable, except perhaps over short time intervals in streams where threatened or endangered species (e.g., galaxiid fishes) are believed to be at risk from *D. geminata* blooms and where no downstream lakes would be affected.

Because the available evidence suggests that blooms are not caused by introductions but rather by environmental factors, research should be aimed at identifying the environmental factors triggering the blooms. For example, a systematic comparison of factors in rivers with and without blooms from around the world using similar methods, especially for low-level nutrient analyses, is needed. In addition, more experiments in which dissolved inorganic P concentrations are manipulated and the response of *D. geminata* is measured in terms of the frequency of dividing cells and stalk production are needed in order to explore the generality of the low P threshold as a trigger of blooms. If low P is the general cause of the blooms, research should be focused on identifying the regional to global factors driving low P, such as N-induced shifts toward P limitation and climate-induced


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shifts in the growing season, timing of springtime runoff, and the rate of snowmelt that can simultaneously reduce P inputs and increase light to rivers, which may interact with local factors linked to blooms, such as rivers draining lake outlets, reservoirs, or a series of beaver dams.

Depending on *D. geminata*'s status as a native invasive or a nonnative invasive, the policies and management will be fundamentally different. To effectively control *D. geminata* blooms, we recommend that efforts be focused on understanding and mitigating the environmental conditions that promote increased stalk production by *D. geminata*. Such a refocus should be more effective at controlling the invasive characteristics of *D. geminata* throughout its contemporary range. If additional research corroborates evidence that low dissolved inorganic P is a proximal cause of *D. geminata* blooms throughout its contemporary range, policies should be aimed at managing the drivers causing declines in P to the threshold that triggers excessive stalk production. In contrast to policies and management of nonnative invasives that are focused on the introduction and spread phases, policies for the control and management of native nuisance species should be focused on the environmental conditions that promote their invasive characteristics.

## Conclusions

Scientific understanding and, therefore, effective management and policy responses to an invasive species depend on knowing whether the ecological and economic damages are caused by its introduction (i.e., for nonnative species) or are the result of changes in environmental conditions that promote invasive characteristics of native species or newly introduced species. An absence of evidence has been used to support the idea that the contemporary blooms of *D. geminata* are caused by introductions to new areas. However, observational and experimental evidence shows that the nuisance or invasive characteristics of *D. geminata* are caused by a specific environmental condition: low P. Research aimed at identifying the generality of the low-P effect on bloom formation and identifying the mechanisms causing low P in rivers around the world can provide support to decision-makers concerning policy, management, and mitigation responses. Knowing the origin of an invasive species can be essential for understanding and managing invasive species, especially if human-induced environmental change exposes more native species to conditions that promote invasive characteristics—particularly among microorganisms that are difficult to detect. We caution against hastily classifying microorganisms that increase in abundance or change their growth form as recently introduced species or genotypes, because policy and management may be misdirected.

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