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The Didymo story: the role of low dissolved phosphorus in the formation of *Didymosphenia geminata* blooms

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We outline, in chronological sequence, the events and findings over 25 years that have shaped our understanding of *Didymosphenia geminata* (Lyngbye) M. Schmidt blooms. Starting with the first appearance of *D. geminata* mats in streams on Vancouver Island in the late 1980s and followed years later by blooms in Iceland, South Dakota and Poland, *D. geminata* blooms were enigmatic for nearly 20 years. Early papers exploring whether blooms were caused by environmental change consistently failed to identify any specific factor(s) associated with their onset. Following the *D. geminata* outbreak in New Zealand in 2004 that seemed to result from an introduction of the species, the possibility that blooms that had previously occurred elsewhere in the world might also be explained by the introduction and movement among watersheds of a new variant with a bloom-forming tendency was touted and widely accepted. Now, however, the identification of very low soluble reactive phosphorus (SRP; below ~2 ppb) as the proximate cause of bloom formation, has led to the more likely explanation that *D. geminata* blooms are the result of large-scale human intervention in climatic, atmospheric and edaphic processes that favour this ultra-oligotrophic species. In this new view, blooms of *D. geminata* are not simply due to the introduction of cells into new areas. Rather, bloom formation occurs when the SRP concentration is low, or is reduced to low levels by the process of oligotrophication. Mechanisms that potentially cause oligotrophication on global and regional scales are identified.

Keywords: *river diatom blooms, rock snot, Didymo, phosphorus limitation, global change, atmospheric N-deposition, N-enrichment of landscapes, dissolved phosphorus*

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The early years (1988–1998)

Modern episodes of *Didymosphenia geminata* (Lyngbye) M. Schmidt blooms in rivers were first systematically documented on Vancouver Island, British Columbia in the late 1980s (Sherbot & Bothwell 1993, Bothwell et al. 2009). British Columbia Ministry of Environment (BCMoE) officials conducting routine water-quality monitoring in rivers downstream of municipalities in 1988 noticed patchy accumulations of slimy looking material covering rocks in the Heber River, upstream of the town of Gold River. One year later, several kilometres of the Heber River were covered in heavy mats. Microscopic examination of the mats revealed the stalk-producing diatom *D. geminata*. The appearance of thick algal mats was unusual because the Heber River, like most rivers on Vancouver Island, is nutrient-poor and extensive algal accumulations upstream of known human nutrient inputs were unprecedented.

In 1993, an *ad hoc* group of biologists and chemists (M. Clark, R. Nordin, J. Deniseger, L. Erikson and C. Wightman) from the BCMoE was established to examine the blooms and determine their causes. Photographs of *D. geminata*-affected rivers on Vancouver Island were taken during site visits (Fig. 1) and included on an early website describing the blooms (http://www.env.gov.bc.ca/wat/wq/didy_bcstrms.html).

Didymosphenia geminata is native to British Columbia, as established by some of the earliest published records of this species (Lord 1866, Cleve 1894–1896). Because *D. geminata* was a native species, a pressing question in the 1980s was whether the blooms on Vancouver Island were new events, or simply newly reported. Because the dense benthic mats were occurring in more remote, sparsely populated areas of the island, this was not an easy question to address. Personal testimonies and scientific grey literature were evaluated. For example, mute evidence was available in the writings of Roderick Haig-Brown (1908–1976) (Fig. 2). Widely recognized as the 20th century's finest and most prolific angler writer, Haig-Brown lived on Vancouver Island most of his adult life and was a pioneering river conservationist. He fished Vancouver Island's rivers and wrote about them for four decades. In *Fisherman's Fall* Haig-Brown (1964) describes two of his favourite rivers,

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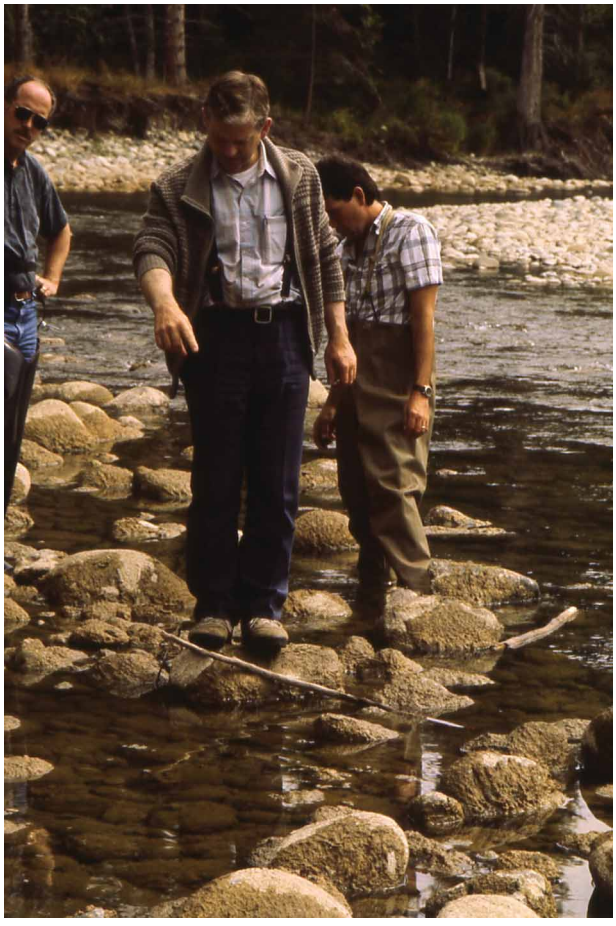


Fig. 1. The British Columbia *Didymosphenia ad hoc* group viewing the *D. geminata* bloom in the Englishman River in 1993.

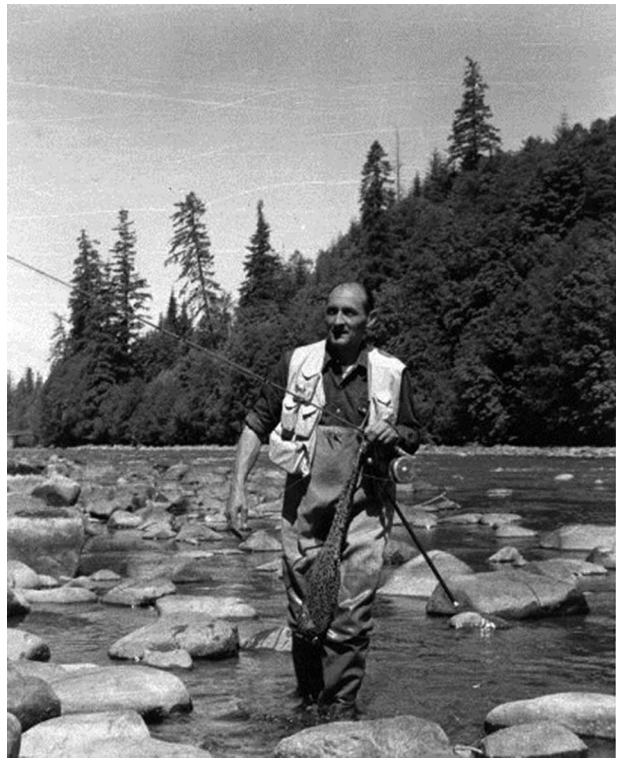


Fig. 2. Roderick Haig-Brown (1908–1976). A pioneer river conservationist, prolific author and resident fly fisherman of Vancouver Island for 42 years. No mention of nuisance benthic algal mats occurs in his writings. (Reproduced with permission of the Haig-Brown Institute.)

the Heber and the Stamp, in both of which *D. geminata* blooms were documented in the 1990s. If these blooms had occurred in his lifetime, Haig-Brown would most likely have seen them and written about them, but no mention appears in his works.

The weakness of Haig-Brown's testimony is that absence of evidence is not evidence of absence. For this reason, confirmation from long-time observers of Vancouver Island rivers was sought. In 1976, the Fish and Wildlife Branch of BCMoE engaged a team of professional fisheries biologists as a Steelhead Snorkel Survey Team (SSST) to conduct annual censuses of steelhead escapement in response to diminishing returns to Vancouver Island rivers. For 13 years, the SSST annually snorkel-surveyed the calibrated reaches of many rivers and filed reports on steelhead numbers. Starting in the early 1990s, the team noted that benthic surfaces were being covered with thick brown mucilaginous mats that had not occurred in the preceding decade (L. Carswell, G. Horncastle, R. Hooton, R. Axford and S. Hay, pers. commun.). Notes from the SSST helped document the development of *D. geminata* proliferations among rivers on Vancouver Island.

In the late 1970s, Fisheries and Oceans Canada conducted a study of the impact of nutrients discharged by fish hatcheries into rivers in British Columbia by quantifying algal biomass and diatom species abundance (Munro et al. 1985). The Puntledge River on Vancouver Island was included in this study. Between 1978 and 1980, *D. geminata* was never sufficiently abundant to make the list of quantifiable diatom taxa, although it was occasionally present (Munro et al. 1985). Starting in 1991 and continuing to the present, *D. geminata* accumulations persist in varying degrees in the Puntledge River. Munro et al. (1985) corroborate that *D. geminata* was present in Vancouver Island rivers prior to 1989, but in low abundance.

The most likely factors for increased benthic algae in streams are typically either eutrophication (i.e., increased concentration of nutrients, most often phosphorus) or declines in the intensity of physical disturbance or scour (Biggs & Close 1989, Biggs 2000). In 1993, we examined water chemistry (BCMoE Environmental Monitoring System Web Reporting) and hydrological (Water Survey of Canada, HYDAT 1992) databases for rivers on Vancouver Island. Although the analysis was hampered by a 3 ppb minimum detection limit for SRP, there was no indication that the onset of blooms resulted from either an increase in SRP

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or benign hydrological conditions (Sherbot & Bothwell 1993).

In the 1990s, ground level increases in solar ultraviolet radiation (UVR) resulting from global ozone depletion were identified as a potential threat to aquatic ecosystems at mid and higher latitudes (Häder & Worrest 1991). Unshaded, shallow, clear water streams were especially vulnerable (Bothwell et al. 1994). Although the inhibition of attached riverine diatom communities by natural UVR was significant, of most relevance was the finding that some species of stalked diatoms in the genera *Gomphoneis* and *Cymbella* appeared to be preferentially favoured under exposure to UV light (Bothwell et al. 1993). *Didymosphenia geminata*, however, was not found in the experiment.

A later, *in situ*, experiment was run in 1995 to assess the deleterious effects of UVR on aquatic insects (Kelly 2001). During a 70-day experiment, diatom samples were collected and enumerated, but at the time, the data were not analysed. We recently analysed the Kelly data. Two-way analysis of variance (ANOVA) revealed no consistent effect of solar UVR on the abundance of *D. geminata* over a 70-day period relative to other diatom taxa ($p = 0.71$) (Fig. 3). Although a positive relationship would have provided a plausible explanation for *D. geminata* blooms, the data do not support this conclusion.

More recent research in New Zealand demonstrated an initial, inhibitory effect of UVR on *D. geminata* cell division that diminished after six days (Kilroy & Bothwell 2011b). Stalk lengths are also often reduced under exposure to UVR (Kilroy and Bothwell 2014). No positive relationship between UVR and *D. geminata* growth has been documented, despite ongoing speculation that a relationship exists (James et al. 2013). Although greater solar exposure can increase *D. geminata* stalk length (Kilroy & Bothwell 2011a) and has been associated with greater bloom development (James et al. 2013), it appears that the UVR portion of the solar spectrum does not play a major role in *D. geminata* blooms (Kilroy & Bothwell 2011b, Kilroy & Bothwell 2014).

The net result of investigating *D. geminata* blooms on Vancouver Island in the early years was that, although it was a native species, the blooms appeared to be a new phenomenon, and there was no obvious change in environmental conditions that might explain them.

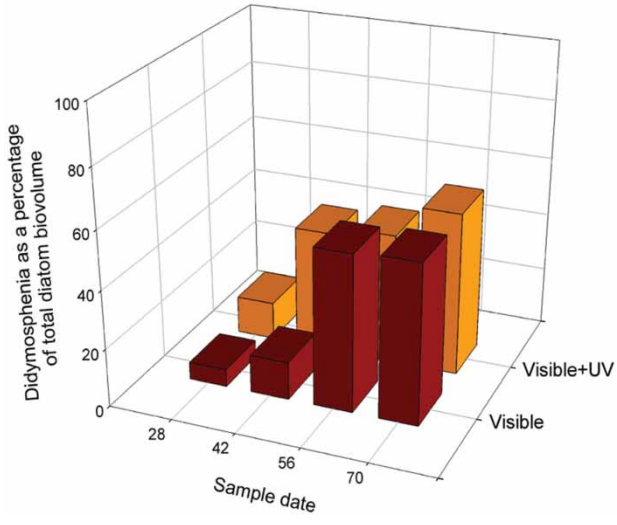


Fig. 3. *Didymosphenia geminata* as a percentage of total diatom biovolume during an *in situ* solar UVR exclusion experiment in the Little Qualicum channel on Vancouver Island during 1995 (Kelly 2001). The presence or absence of UVR had no affect on the abundance of *D. geminata* relative to other diatom taxa (two-way ANOVA, $p = 0.71$).

On the boots of fishermen

The onset of *D. geminata* blooms in New Zealand in 2004 was widely attributed to the incursion of a new species (Kilroy 2004). This suggestion reignited questions about the cause of blooms on Vancouver Island 15 years previously. Was the explanation for blooms that resulted from an introduction in New Zealand also applicable to Vancouver Island? *Didymosphenia geminata* was a native species in British Columbia, but could a new bloom-forming variant have been introduced in the 1990s? Might this be the reason we had been unable to make sense of the blooms in the northern hemisphere?

On Vancouver Island, the British Columbia Steelhead Harvest Questionnaire database was used to quantify angler activity on selected rivers between 1968 and 2003 and revealed a three- to fourfold increase in angler days on some rivers in the mid-1980s leading up to the *D. geminata* blooms (Bothwell et al. 2009). Increased river use coincided with the commercial introduction of felt-soled waders, the expansion of the guided fishing industry, and an increase in the number of visiting anglers fishing the rivers of Vancouver Island. The analysis of these data entitled, 'On the Boots of Fishermen: The History of Didymo Blooms on Vancouver Island, BC' was published in *Fisheries* (Bothwell et al. 2009), with the statement:

> ….all of the evidence suggesting that recreational fishermen have played a role in the movement of Didymo regionally and globally is circumstantial.

Nevertheless, the publication was widely accepted as an important step in initiating management actions aimed at controlling the spread of aquatic invasive species. Yet, the explanation for the spatial and temporal occurrence of blooms of *D. geminata* as the result of human vectors was based on coincidental timing.

The Didymo trilogy

Early in the incursion of *D. geminata* into New Zealand, it became clear that bloom formation must involve more than the simple introduction of cells into new areas. The observation that blooms did not form in spring-fed creeks

discharging into *D. geminata*-affected rivers on the South Island, in spite of repeated introduction of cells, was demonstrated multiple times (Sutherland et al. 2007). To address experimentally the role of environmental factors (light intensity and nutrient concentration of N and P) leading to bloom formation, a flume apparatus was built on the bank of the *D. geminata*-affected Waitaki River, adjacent to the confluence with the *D. geminata*-free, Otiake Spring Creek (Fig. 4). This facility was utilized in a collaborative research project between Environment Canada (EC) and the New Zealand Institute for Water and Atmospheric Research (NIWA) during 2008–2010. Results from the NIWA–EC studies were published (Bothwell & Kilroy 2011, Kilroy & Bothwell 2011a, Kilroy & Bothwell 2012). We refer to these three papers as the 'Didymo Trilogy' because each paper contains solutions to pieces of the puzzle and, collectively, they provide the evidence that the proximate cause of *D. geminata* blooms in rivers is low concentration of P. We outline the 'Didymo Trilogy' as three chapters in our understanding.

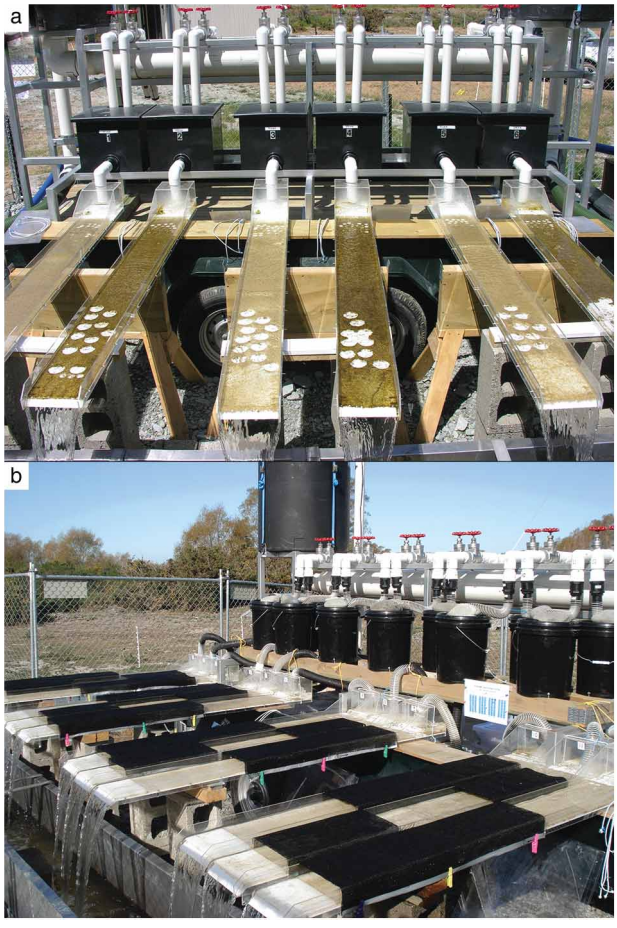


Fig. 4. The experimental flume apparatus used during the collaborative research project between EC and NIWA during 2008–2010 was located on the bank of the Waitaki River, South Island, New Zealand, adjacent to the confluence with the Otiake Spring Creek. (a) The initial design in 2008 had six flumes, all initially colonized with *D. geminata* using Waitaki River water. Subsequently, three of the flumes were shifted to Otiake Spring Creek water (treatment), while the other three remained as controls and continued to receive Waitaki River water (details in Bothwell & Kilroy 2011). (b) In 2009–2010, a total of 12 flumes were employed to test additions of P or N and light intensity using shading cloth (details in Bothwell & Kilroy 2011; Kilroy & Bothwell 2011a).

Chapter 1: phosphorus limitation (Bothwell & Kilroy 2011)

The summary points from this paper are:

(1) The frequency of dividing cells (FDC) is used as a metric for P-limited growth rates in *D. geminata*. FDC has been used to measure aquatic microbial growth for decades, but its application to *D. geminata* was key to understanding the blooms.
(2) Exposed to high concentrations of P, *D. geminata* cells divide rapidly for short periods, but colonies and blooms eventually dissipate.
(3) Experiments conducted year-round identified a continuing high level of P-limitation in *D. geminata in situ* while cells remained dominant in the Waitaki River.
(4) FDC was the same whether or not cells were associated with colonies and we concluded that *D. geminata* cells do not necessarily access P from within benthic mats.

Chapter 2: environmental control of stalk length (Kilroy & Bothwell 2011a).

The summary points from this paper are:

(1) When cell division rates are low, the much longer stalks characteristic of blooms are produced. Such diversion of photosynthetically fixed carbon into extracellular compounds under conditions of nutrient limitation is characteristic of some diatoms (Myklestad 1995).
(2) Higher light conditions also result in longer stalks.

Chapter 3: relation of cell growth rates and bloom formation to dissolved phosphorus concentrations (Kilroy & Bothwell 2012)

The summary points from this paper are:

(1) Synoptic surveys of rivers on South Island, New Zealand show that the distribution of *D. geminata* blooms can be predicted from the SRP concentration. Blooms do not form if the mean SRP concentration over a 24-month period (monthly sampling) exceeds ~2 ppb (Fig. 5).
(2) A direct positive relationship exists between ambient SRP concentration in the water and *D. geminata* FDC (Fig. 6a), whereas an inverse relationship

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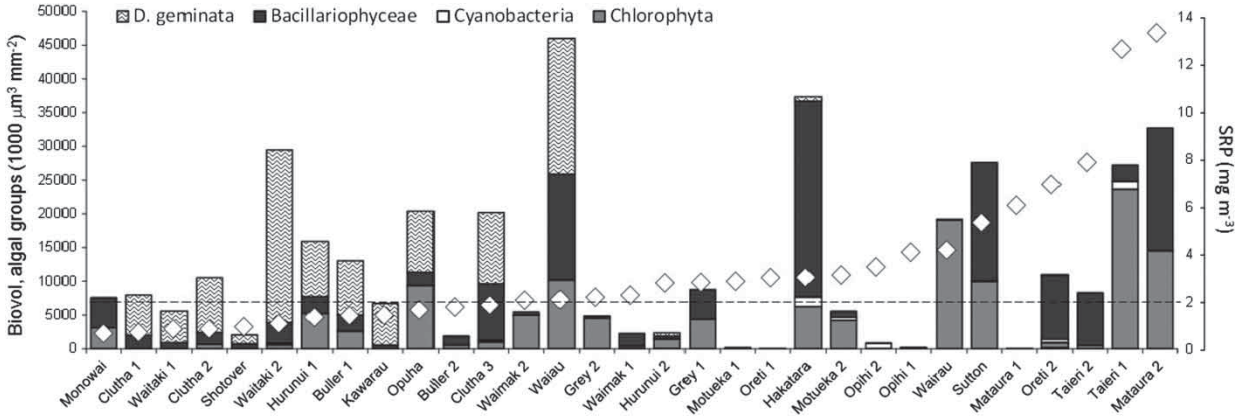


Fig. 5. Algal biovolume expressed as standing crop index (% cover × mat thickness in mm) at each of 31 South Island, New Zealand, river sites surveyed between January and March 2010, in terms of broad algal groups and *D. geminata*, with mean SRP (diamonds) shown for each river. The dashed horizontal line indicates 2 ppb SRP.

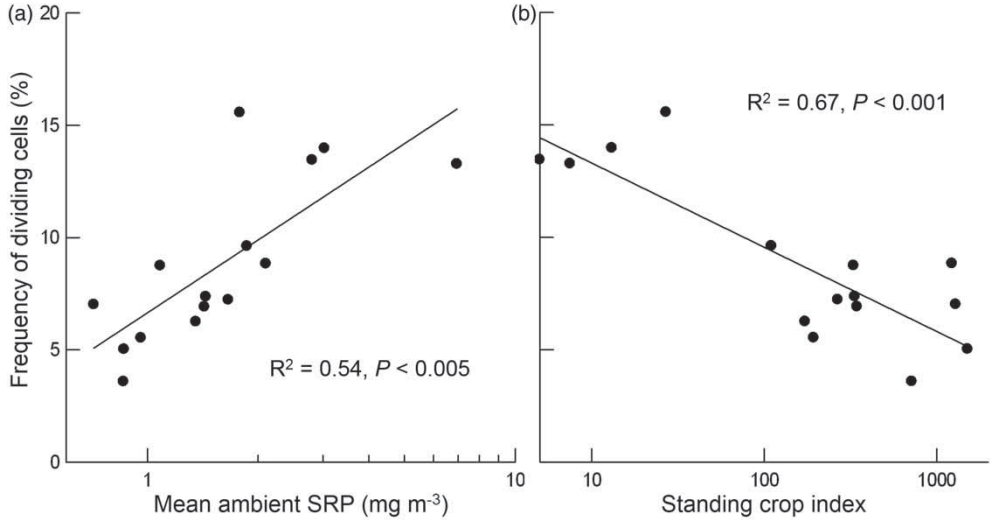


Fig. 6. Relationship between (a) FDC and mean ambient SRP and (b) FDC and standing crop index at 15 South Island river sites where *D. geminata* was present.

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exists between FDC and *D. geminata* biovolume, measured as a standing crop index (Fig. 6b). This is also a likely explanation for the absence of *D. geminata* on the North Island of New Zealand (Kilroy & Unwin 2011, Rost et al. 2011) where nearly all rivers have naturally high SRP, >2 ppb, shown to prevent bloom establishment in rivers on the South Island (Kilroy & Bothwell 2012).

(3) A transect across a braid in the Waitaki River just below a spring tributary indicated that the SRP concentration that inhibits blooms might even be lower (<1 ppb) than indicated in the synoptic survey of South Island.

Our epiphany

The publications that we refer to as the 'Didymo Trilogy' made clear to us that the proximate cause of blooms or, more precisely, excessive extracellular stalk production, is low P. There is precedence for a mucopolysaccaride production response to low P. For example, photosynthetic release of structural or non-structural exudates is a common stress response by some diatoms to low nutrient conditions (Hoagland et al. 1993, Myklestad 1995). Moreover, the most rapid increase in diatom-specific growth rate occurs below 1 ppb dissolved P, so changes in dissolved P below 1 ppb are highly relevant to diatom cell division (Bothwell 1988, 1989). The unexpected conclusion is that *D. geminata* blooms do not occur in spite of P limitation, they occur because of it! Stalk production in response to very low P may be a strategy to move cells out of the benthic boundary layer and into the water column where there is greater delivery of growth-limiting P. We propose that P concentrations in relatively unaffected rivers around the world are declining and *D. geminata* blooms are actually the result of that decline, not primarily the result of recent introduction.

At this point, it is important to highlight the difference between blooms of *D. geminata* and geographic distribution of this species. New Zealand is the best example of an introduction of *D. geminata* (Kilroy & Unwin 2011). However, while the presence of cells is obviously prerequisite, introduction alone is not the cause of bloom formation.

The ultimate causes of *D. geminata* blooms

With low SRP identified as the proximate cause of *D. geminata* blooms, we propose four mechanisms operating at global or regional scales that could potentially result in a decline of P, i.e., oligotrophication, entering fluvial systems. We outline the following as hypotheses of the potential ultimate causes of *D. geminata* blooms: (1) atmospheric deposition of reactive nitrogen resulting from the burning of fossil fuels and urbanization; (2) climate-induced shifts in the timing of snowmelt and growing season that decreases P inputs to rivers; (3) N-enrichment of landscapes during agricultural and silvicultural activities that result in greater retention of terrestrial P; and (4) a decline in marine-derived nutrients, particularly P, resulting from widespread depletion in spawning salmon. Although these processes do not apply to all regions, they are not mutually exclusive and could act synergistically. These processes are in need of further investigation for their role in driving blooms of *D. geminata*.

The above potential ultimate drivers for the formation of *D. geminata* blooms are consistent with the worldwide occurrence of blooms. In the case of Vancouver Island, it is now known that the onset of *D. geminata* blooms in the early 1990s followed the commencement of an island-wide annual urea-N fertilization silvicultural programme that was among the largest of its kind in North America (British Columbia Ministry of Forests, Lands, and Natural Resource Operations; http://www.for.gov.bc.ca/hfp/publications/00001/2–2-silv-stand-index.htm). Increased N inputs to landscapes will likely lead to increased P assimilation, reducing its availability for run-off into streams. A detailed discussion of these processes is presented elsewhere.

In addition to the large-scale processes we outline as the ultimate drivers of oligotrophication, understanding that low SRP is the proximate cause of bloom formation, affords new interpretations of how local-scale factors, which potentially alter P concentration, can explain smaller scale spatial variability of blooms. For example, the well-known tendency for *D. geminata* bloom formation to occur below lakes and dam outlets (Kirkwood et al. 2009) takes on a new significance in the light of dissolved P depletion in lake surface waters during the summer. Likewise, variations in *D. geminata* bloom formation along river channels have been shown to follow regions of upwelling and downwelling exchange with the hyporheic zone, with blooms being absent in zones of upwelling, nutrient-rich, hyporheic water, but forming in potentially P-depleted downwelling regions (Wyatt et al. 2008). Low dissolved P as the proximate cause of *D. geminata* bloom formation provides a parsimonious explanation for *D. geminata* blooms across spatial scales.

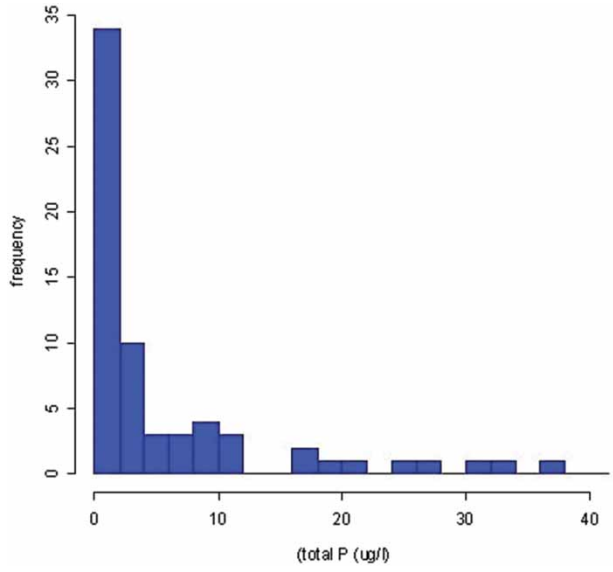


Fig. 7. The relationship between the frequency of occurrence of *D. geminata* cells and total phosphorus concentration. Data from the EPA Environmental Monitoring and Assessment Programme (EMAP), 2000–2003. Taken from Spaulding & Elwell (2007).

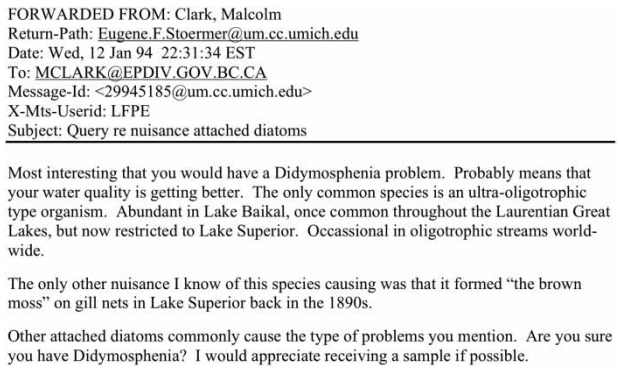
As we wrote elsewhere, '*Didymosphenia geminata* blooms end when cell division rates are not limited by P, and blooms do not begin unless these rates are P-limited' (Bothwell et al. 2012). Much of the focus on *D. geminata* has been on identifying favourable potential-habitat conditions, not on what causes bloom formation. Once the suite of physical (higher light, low turbidity, stable substratum and flow) and chemical (specific pH range, minimum Ca and Si, maximum Na and Cl) prerequisites are met, we have shown that it is the concentration of soluble available P that explains the timing and spatial distribution of blooms where *D. geminata* cells are present.

Why was low P overlooked?

Parameters associated with the presence of *D. geminata* were outlined for the United States (Spaulding & Elwell 2007). Using data from the EPA Environmental Monitoring and Assessment Programme, Spaulding & Elwell illustrated that *D. geminata* is most frequently found in low-nutrient water (Fig. 7). Why was the simplest explanation for the increase in *D. geminata* abundance and the appearance of blooms as low P missed? A likely answer to this question is that aquatic biologists typically associate higher algal biomass with increases in nutrients, not decreases.

However, Eugene F. Stoermer, voiced the possibility of low phosphorus. In 1994, he was contacted by the *Didymosphenia ad hoc* group in British Columbia. His response to their query was prescient, indicating that he thought that the

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FORWARDED FROM: Clark, Malcolm
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Date: Wed, 12 Jan 94 22:31:34 EST
To: MCLARK@EPDIV.GOV.BC.CA
Message-Id: <29945185@um.cc.umich.edu>
X-Mts-Userid: LFPE
Subject: Query re nuisance attached diatoms

Most interesting that you would have a Didymosphenia problem. Probably means that your water quality is getting better. The only common species is an ultra-oligotrophic type organism. Abundant in Lake Baikal, once common throughout the Laurentian Great Lakes, but now restricted to Lake Superior. Occassional in oligotrophic streams world-wide.

The only other nuisance I know of this species causing was that it formed "the brown moss" on gill nets in Lake Superior back in the 1890s.

Other attached diatoms commonly cause the type of problems you mention. Are you sure you have Didymosphenia? I would appreciate receiving a sample if possible.

Fig. 8. Email message from Eugene F. Stoermer (1934–2012) on 12 January 1994 responding to a query from Malcolm Clark of the *Didymosphenia ad hoc* group in British Columbia about nuisance diatom blooms in rivers on Vancouver Island.

nuisance *D. geminata* blooms on Vancouver Island probably meant that the water quality in rivers was improving, that is, that P was declining (Fig. 8). Although Gene's view of exotic diatom species later changed (Smol & Stoermer 2010), his initial reaction to the nuisance blooms of *D. geminata* on Vancouver Island is consistent with our recent research, indicating that it is actually low P that causes the blooms. It is also consistent with Gene's recollection that *D. geminata* was once common throughout the Laurentian Great Lakes, but following decades of eutrophication it is now restricted to Lake Superior (Fig. 8).

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