Blooms of benthic diatoms in phosphorus-poor streams

During the past 50 years, freshwater ecologists have mostly attributed massive accumulations of algal biomass in lakes and rivers to high nutrient inputs. While researching the role that phosphorus (P) plays in increasing diatom biomass in rocky-bottomed rivers, I (MLB) was puzzled by the presence of thick mats ("blooms") of the benthic diatom *Didymosphenia geminata* in low-nutrient rivers with no obvious evidence of a pollution source (Figure 1a). *D geminata* has long been associated with nutrient-poor conditions and is native to but historically rare in North America (Figure 1b). Beginning in the early 1990s, thick and visually unappealing mats of the diatoms appeared suddenly in streams that drained pristine watersheds, despite no obvious increase in pollution. The basic natural history of this species was unknown and the origin of the blooms remained an unsolved mystery for more than 20 years.

After the species was introduced to New Zealand, *D geminata* blooms began to be observed there in 2004 (Kilroy 2004), but early evidence suggested that more was involved than a simple movement of cells into previously uninhabited areas. For instance, when transplanted into spring-fed creeks that were tributaries of rivers already infested with *D geminata*, the diatoms failed to flourish (Sutherland *et al.* 2007) even though nutrient levels, including P, were higher in the creeks than in the rivers. These creeks also appeared to be physically suitable habitats for the species. Because *D geminata* did not form blooms when P concentrations were high, it was hypothesized that a different chemical constituent of stream water was critical for bloom formation. A carefully conducted study was undertaken in New Zealand in search of a "silver bullet" in spring water that would prevent *D geminata* establishment and might be useful for controlling the blooms in other rivers.

I designed a riverbank flume apparatus that would allow settled *D geminata* cells to be bathed in either river water or spring water without first having to be physically transplanted. Once *D geminata* cells had attached on the bottoms of all flumes exposed to river water, the source of water for some populations was gradually switched to the spring water. I assumed that the newly settled cells would perish, but something unexpected happened (Bothwell and Kilroy 2011). After being exposed to spring water for 8 days, 40% of *D geminata* cells were in late stages of cell division compared to only 10% of the cells with continued exposure to river water (Figure 2). *D geminata* cells seemed to thrive in spring water and a follow-up experiment confirmed that, when exposed to spring water, cell division rates were elevated because of the higher nutrient levels, especially dissolved P (Bothwell and Kilroy 2011).

So, why would higher P concentrations have a positive impact on cell division but a negative impact on bloom development? This paradox was clarified by an additional observation – that *D geminata* populations with rapidly dividing cells tended to have much shorter stalks, which would adversely affect bloom development.

Observations on the frequency of cellular division allowed us to explore the influence of P on *D geminata* growth and mat development in rivers. On the South Island of New Zealand, river surveys showed the counter-intuitive, inverse relationship between low rates of *D*

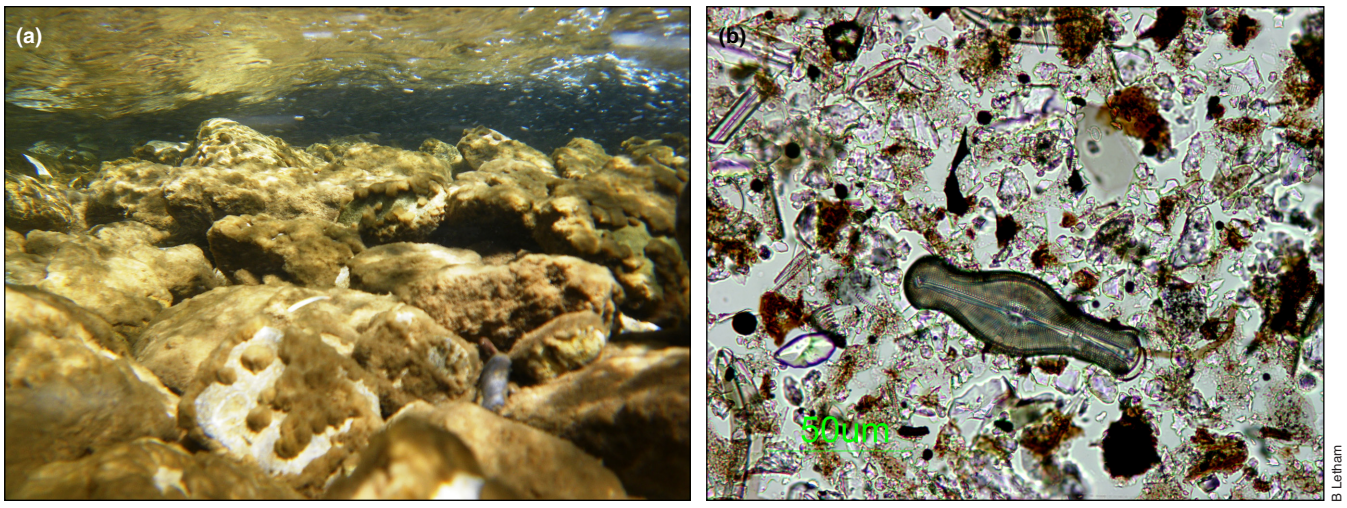


Figure 1. *(a)* Didymosphenia geminata *mat formation in North York Creek, a nutrient-poor stream in the Canadian Rocky Mountains (1600-m elevation). (b) A single specimen of* D geminata *was found in seven sediment cores taken 7 km WNW of Prince Rupert, British Columbia. The sediment layer in which this* D geminata *specimen was found dated to between 11,000 and 12,000 calendar years ago (Letham* et al. *2016).*

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geminata cell division and the more extensive coverage and thickness of *D geminata* mats on river bottoms (Kilroy and Bothwell 2012). For mats to develop, *D geminata*'s extracellular stalks – which are composed of polysaccharides (Hoagland *et al.* 1993) – need to elongate, but frequent cell division results in shorter stalks (Kilroy and Bothwell 2011) and a lower probability of benthic mat formation. By increasing the rates of cell division, high P concentrations appear to leave little time for stalks to grow longer and so mats fail to develop.

The presence of *D geminata* blooms in nutrient-poor conditions challenges the long-held view of the relationship between limiting nutrients and algal production in freshwater ecosystems. The opposing effects of P availability on cell division versus non-cellular mat development suggest a strategy that is more reminiscent of terrestrial plants reallocating energy into tissues and structures (eg roots or shoots) needed to access limiting resources. Production of long extracellular stalks allows cells to have better access to nutrients in free-flowing water; this enhanced accessibility is one of the longstanding explanations for the adaptive significance of diatom stalk production (Hudon and Bourget 1981). The explanation for higher algal-derived carbon in a declining P regime is the shunting of carbon into non-P-containing stalks.

Unlike algal "blooms" in the limnological lexicon, *D geminata* mat formation does not necessarily represent increased cellular biomass. An even greater paradox is that, because an excessive P supply results in the decline of mats (Kilroy and Larned 2016), the *D geminata* mats produced in response to low P must remain P-limited to continue to dominate benthic algal communities. A careful balance between P acquisition and allocation of growth to stalks is required for *D geminata* to remain the dominant algal taxon in a stream ecosystem. While lower P concentrations provide an explanation for why *D geminata* mats form, whether or not dissolved P in pristine streams worldwide is declining remains unknown (Taylor and Bothwell 2014). Surprisingly, studying the natural history of *D geminata*'s cellular division has been the key to deciphering the larger-scale natural history of mat formation and the recent dominance of this organism when P concentrations are low.



Figure 2. *(a) A non-dividing* D geminata *cell; (b)* D geminata *undergoing cell division; (c)* D geminata *cell division complete, but new daughter cells remain attached in a "doublet" stage; (d) after division and separation, daughter cells remain attached to the same stalk until new stalks are produced by each cell. Under low light, cells can be "trapped" in this stage because high photosynthetic rates are needed for new stalk production.*

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