Rock Snot: An Annotated Bibliography of the Science on *Didymosphenia geminata*

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Cover image from Lavery et al. (2014)

Summary

1. *Didymosphenia geminata*, hereafter “Didymo”, is a stalk-forming freshwater diatom or alga that can develop thick benthic mats, or blooms.

2. Didymo has a relatively expansive native range within and outside of the United States (Blanco and Ector 2009; Taylor and Bothwell 2014).

3. Didymo can be present for decades or more without blooming (Kunza et al. 2018), and blooms can occur in streams rarely or never visited by humans (Schweiger et al. 2011).

4. Didymo can be introduced to new streams, and humans have been implicated as a vector of dispersal (Kilroy and Unwin 2011; Bothwell et al. 2009; but see Taylor and Bothwell 2014).

5. Contrary to most algae, Didymo becomes a nuisance at relatively low nutrient concentrations, when the diatom lengthens its stalk and blooms (Bothwell and Taylor 2017).

6. Two hypotheses have been proposed to explain a rapid, global increase in the incidence of Didymo blooms:1) widespread introduction of Didymo to previously unoccupied waters and 2) response by pre-existing Didymo populations to changes in environmental conditions (Bothwell et al. 2009; Taylor and Bothwell 2014; Kunza et al. 2018).

7. Multiple lines of evidence (e.g., Kilroy and Bothwell 2012; Bothwell et al. 2014; James et al. 2015) suggest phosphorous limitation is the primary driver of Didmyo blooms. Those same lines of evidence suggest that, whether or not Didymo is endemic to a stream, a bloom will not occur unless soluble reactive (i.e., dissolved) phosphorous levels are extremely low (typically < 2.0 ppb). Nevertheless, research suggests that phosphorous limitation is not the only driving factor of Didymo blooms (Kirkwood et al. 2007; Kunza et al. 2018).

8. Didymo blooms have been associated with a number of different changes in benthic macroinvertebrate communities—for example, increases in invertebrate density (Gillis and Chalifour 2010; Larned and Kilroy 2014) and shifts away from mayflies, stoneflies, and/or caddisflies (Anderson et al. 2014; Jellyman and Harding 2016; Clancy et al. 2021), which are collectively considered to be preferred prey for trout and indicators of a healthy stream.

9. Peer-reviewed studies of Didymo-fish relationships are few in number and fail to reveal clear and consistent impacts of Didymo on trout. For example, while one group of researchers found that trout were more abundant in the presence than absence of Didymo blooms (Clancy et al. 2021), another group found that trout biomass was comparable among streams with and without Didymo (James et al. 2016), and a third group observed a negative relationship between Didymo biomass and trout biomass (Jellyman and Harding 2016).

10. Soaking waders and boots in a 5% dish soap solution for 1-minute can kill > 90% (but < 100%) of Didymo cells (Root and O’Reilly 2012). Decontamination procedures are more effective at killing free-floating Didymo cells than those attached to clumps of material.

Editor's Note

The following pages include an annotated bibliography of sources on Didymo. Because the peer review process sets a standard for, and improves the quality of, scientific communication, only articles from peer-reviewed journals are included. Citations are listed in chronological order to help illustrate the evolution of science around Didymo. For reader convenience, all nutrient concentrations have been converted into the single common unit of parts per billion (ppb;1 ppb = 1 μg/L). A glossary of terms and definitions is included at the back of the document.

References (Available here)

Kirkwood, A. E., T. Shea, L. J. Jackson, and E. MCauley. 2007. *Didymosphenia geminata* in two Alberta headwater rivers: an emerging invasive species that challenges conventional views on algal bloom development.

One of the early published studies on Didymo, Kirkwood et al. (2007) evaluated relationships between Didymo and environmental parameters in two Canadian rivers. Of all the factors considered, mean discharge was the best-substantiated predictor of Didymo biomass and explained approximately 30% of the variation in Didymo biomass. Moreover, Didymo biomass decreased as mean discharge increased. Kirkwood and others (2007) suggested that streamflow regulation might be a means of controlling and/or preventing Didymo blooms.

Blanco, S., and L. Ector. 2009. Distribution, ecology, and nuisance effects of the freshwater invasive diatom *Didymosphenia geminata* (Lyngbye) M. Schmidt: a literature review. Nova Hedwigia 88:347-422.

Blanco and Ector (2009) conducted an exhaustive literature review to investigate the current (as of 2009) and historical range of Didymo across the world. The search revealed tens, if not hundreds, of accounts of Didymo in North America, with observations and fossil records dating back the 1800s and beyond, respectively. The authors concluded that the native range of Didymo is more expansive than is commonly reported and that Didymo is being documented with increasing frequency.

Miller, M. P., D. M. McKnight, J. D. Cullis, A. Greene, K. Vietti, and D. Liptzin. 2009. Factors controlling streambed coverage of *Didymosphenia geminata* in two regulated streams in the Colorado Front Range.

Miller and others (2009) used a pair of dam-regulated Colorado streams to examine the relationship between Didymo and environmental factors. Didymo abundance was negatively associated with streambed disturbance and total dissolved phosphorous but unaffected by dissolved inorganic nitrogen, stream temperature, conductivity, pH, and total suspended solids. The authors suggested that both phosphorous concentration and bed movement warranted further investigation as potential Didymo control mechanisms.

Bothwell, M. L., D. Lynch, H. Wright, and J. Deniseger. 2009. On the Boots of Fishermen: The History of Didymo Blooms on Vancouver Island, British Columbia, Fisheries, 34:8, 382-388.

In their article in Fisheries magazine, Bothwell et al. (2009) recounted one of the first documented nuisance blooms of Didymo in North America—an event that occurred in the late-1980 on Canada's Vancouver Island. The authors outlined several lines of evidence that suggested the Didymo blooms on Vancouver Island were more likely owing to angler introduction than to changes in environment: 1) blooms in streams did not coincide with notable changes in the physical and chemical composition of those streams; 2) blooms occurred within or adjacent to reaches frequented by anglers; 3) blooms occurred around the time that Vancouver Island saw a three-fold increase in non-resident anglers; and 4) blooms occurred around the time that felt-soled wading boots, which have been implicated as a vector of transport for aquatic species, became popular among fisherman. Based on local and global observations, Bothwell et al. (2009) concluded that, while Didymo might occupy a broad native range, Didymo blooms are likely owing to the introduction of non-native or invasive lineages of the diatom.

Kumar, S., S. A. Spaulding, T. J. Stohlgren, K. A. Hermann, T. S. Schmidt, and L. L. Bahls. 2009. Potential habitat distribution for the freshwater diatom *Didymosphenia geminata* in the continental US. Frontiers in Ecology and Environment 7:415-420.

Kumar et al. (2009) used Didymo presence-absence and corresponding environmental data to develop a series of models for predicting the U.S. distribution of Didymo. Their best-performing model predicted that the environments most suitable to Didymo are located primarily in the Colorado Rocky Mountains, northwestern Wyoming, western Montana, and northern Idaho. They found that, while Didymo will occupy variable environments, probability of occurrence is greatest in cool, high-elevation headwater streams where groundwater is a major component of total streamflow.

Gillis, C-A, and M. Chalifour. 2010. Changes in the microbenthic community structure following the introduction of the invasive algae *Didymosphenia geminata* in the Matapedia River (Québec, Canada). Hydrobiologia 647(1):63-70.

In eastern Canada, Gillis and Chalifour (2010) monitored benthic macroinvertebrate communities at three sites affected and one site unaffected by Didymo. Macroinvertebrate density was significantly higher in Didymo-impacted sites than in non-impacted sites. No statistically significant differences were observed in proportions of EPT taxa (mayflies, stoneflies and caddisflies), community diversity and balance, or richness.

Kilroy, C. and M. Unwin. 2011. The arrival and spread of the bloom-forming, freshwater diatom, *Didymosphenia geminata,* in New Zealand. Aquatic Invasions 6(3):249-262.

Kilroy and Unwin (2011) used data, literature, and survey results to 1) explore the hypothesis that Didymo was recently introduced to New Zealand and 2) examine the spread of Didymo in New Zealand subsequent to its presumed introduction. They concluded, based on the lack of evidence for pre-existing Didymo populations, that the freshwater diatom was introduced (i.e., not endemic) to New Zealand. Further, they concluded that of the 12 transport vectors considered, anglers were the most likely path by which Didymo spread across the South Island.

Schweiger, E. W, I. W. Ashton, C. C. Muhlfield, L. A. Jones, and L. L. Bahls. 2011. The distribution and abundance of a nuisance alga, *Didymosphenia geminata*, in streams of Glacier National Park: climate drivers and management implications. Park Science 28(2):88-91.

Using Glacier National Park as a study area, Schweiger et al. (2011) examined contributing factors to Didymo abundance. Based on data collected from 49 streams, the authors concluded that Didymo occupied 64% of, but was blooming in only 5% of, the Park's total stream length. Didymo abundance was positively associated with summer stream temperature but negatively associated with total nitrogen and distance below a lake. Schweiger et al. (2011) found no evidence of a relationship between human activity and Didymo abundance and noted that Didymo blooms were frequently observed at locations seldom if ever accessed by Park visitors.

Root, S., and C. M. O'Reilly. 2012. Didymo Control: Increasing the Effectiveness of Decontamination Strategies and Reducing Spread. Fisheries 37(10):440-448.

Root and Reilly (2012) conducted an experiment to evaluate which of several common wader disinfection methods was most effective at killing Didymo. Among the disinfection treatments tested, dish detergent (5% Dawn, 5% Green Works) and bleach (2% Clorox) solutions were most effective; however, none was 100% effective. Effectiveness did not differ between one- and five-minute submersion times, and all treatments were significantly more effective at killing free-floating than stalk- or clump-attached Didymo cells. The authors recommended that anglers dip wading gear into a 5% dish soap solution for 1 minute.

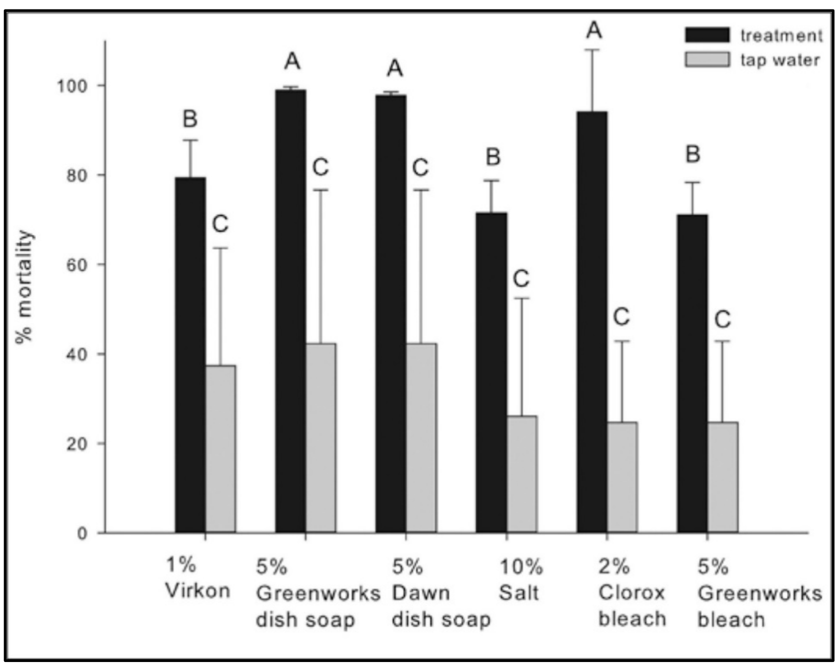

Figure from Root and O'Reilly (2012). "Effectiveness of decontamination treatments compared to a control of tap water. Treatments were significantly more effective than tap water. Letters show significant differences among the treatments. Data are means (n = 10) with standard error."

Kilroy, C., and M. L. Bothwell. 2012. *Didymosphenia geminata* growth rates and bloom formation in relation to ambient dissolved phosphorous concentration. Freshwater Biology 57:641-653.

Kilroy and Bothwell (2012) employed a number of different techniques to examine the relationship between Didymo and phosphorous availability. The authors noted that, across 31 sites and 19 rivers in New Zealand, dense Didymo coverage occurred primarily at locations where dissolved reactive phosphorous (DRP) concentrations were < 2 ppb. Didymo was observed at only one site where the DRP concentration exceeded 4 ppb. The authors also noted that blooms occurred when a Didymo community was intentionally deprived of nutrients (nitrogen and phosphorous) for two weeks. Collectively, findings by Kilroy and Bothwell (2012) suggest that phosphorous availability, or lack thereof, is a primary driver of Didymo blooms.

Larned, S. T., and C. Kilroy. 2014. Effects of *Didymosphenia geminata* removal on river macroinvertebrate communities. Journal of Freshwater Ecology 29(3): 345-362

Larned and Kilroy (2014) observed that some of the prior associations between Didymo and benthic macroinvertebrates could have been inadvertently based on circumstantial evidence rather than mechanistic relationships. To examine the direct effects of Didymo on benthic macroinvertebrates, they conducted a paired before-after, control-impact experiment in three New Zealand streams, all which were affected by Didymo. Specifically, the research team removed Didymo mats from sections of each stream and then tested for Didymo (or Didymo-removal) effects on benthic macroinvertebrate communities. Their results generally aligned with findings from prior studies on the matter: following Didymo removal, invertebrate densities decreased; the relative contribution of mayflies, stoneflies, and caddisflies increased; and density of a dominant Dipteran decreased. One of the other findings by Larned and Kilroy (2014) was that bug communities differed more among streams and time periods than between control and impact sites within streams.

Anderson, I. J, M. K. Saiki, K. Selheim, and J. E. Merz. 2014. Differences in Benthic Macroinvertebrate Assemblages Associated with a Bloom of *Didymosphenia geminata* in the Lower American River, California. The Southwestern Naturalist 59(3):389-395.

In a study of the American River below Nimbus Dam (California), Anderson et al. (2014) compared the benthic macroinvertebrate composition from a stream reach affected by Didymo to that of nearby reach unaffected by Didymo. Whereas the reach with abundant Didymo contained higher numbers of midges, scuds, leaches, and microcaddisflies, the reach with little to no Didymo contained higher numbers of bugs from the orders Ephemeroptera (mayflies), Plecoptera (stoneflies), and Trichoptera (caddisflies). Overall, taxonomic diversity was higher in the reach where Didymo was rare or absent than in the reach where Didymo was abundant. The authors tentatively concluded that Didymo affected the benthic macroinvertebrate community in the lower American River.

Bothwell, M. L., B. W. Taylor, and C. Kilroy. 2014. The Didymo story: the role of low dissolved phosphorus in the formation of *Didymosphenia geminata* blooms. Diatom Research 29(3):229-236.

In this 2014 paper, arguably one of the most important to date for our understanding of Didymo ecology, Bothwell and others summarized the state of knowledge around Didymo and revealed a self-described epiphany about the likely cause of Didymo blooms (the epiphany is preceded by an outlay of contributing points and papers [see Bothwell and Kilroy 2011; Kilroy and Bothwell 2011; Kilroy and Bothwell 2012]). The authors concluded that Didymo blooms occur when phosphorous (P) concentrations are extremely low (dissolved P < 1 ppb) and the diatom builds its stalk to access P in the water column. Further, the authors suggested that the onset of Didymo blooms in relatively pristine or oligotrophic systems is not so much resulting from introduction as it is owing to a decline in dissolved or soluble reactive P. Moreover, Bothwell et al. (2014) noted that introduction of Didymo is not sufficient cause in itself to trigger a Didymo bloom; rather, blooms are triggered by P limitation. The authors go on to identify four hypotheses for declining availability of soluble P: 1) atmospheric deposition of reactive nitrogen (N), 2) climate-induced shifts in the timing of snowmelt and growing season reduces P inputs to rivers, 3) N enrichment of landscapes results in greater retention of terrestrial P, and/or 4) marine-derived sources of P are reduced as a consequence of declining salmon runs.

Taylor, B. W., and M. L. Bothwell. 2014. The Origin of Invasive Microorganisms Matters for Science, Policy, and Management: The Case of *Didymosphenia geminata*. BioScience 64(6):531-538.

Although the article by Taylor and Bothwell (2014) framed Didymo in the context of policy and management, it reviewed several hypotheses behind the simultaneous, worldwide occurrence of Didymo blooms. The authors concluded, based on several presented lines of evidence, that recent blooms were more likely the result of environmental change than of introduction. Accordingly, they suggested that research and management should focus more on identifying the environmental triggers of Didymo blooms than on attempting to stop the spread of Didymo. Taylor and Bothwell (2014) added that the likely environmental trigger of Didymo blooms is low levels of phosphorous.

Table from Taylor and Bothwell (2014). "Locations of fossil or historical records of *Didymosphenia geminat*a cells and contemporaneous *D. gemin*ata 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*

James, D. A., M. L. Bothwell, S. R. Chipps, and J. Carreiro. 2015. Use of phosphorous to reduce blooms of the benthic diatom *Didymosphenia geminata* in an oligotrophic stream. Freshwater Science 34(4):1272-1281.

In the Black Hills of South Dakota, James et al. (2015) conducted two experiments to test complementary hypotheses that Didymo blooms occur only at low levels of dissolved phosphorous (P) and that P enrichment should thus reduce Didymo biomass. Their study reach, which was located less than 5 km downstream of a reservoir, had for several years been affected by Didymo blooms. Doubling P concentrations above baseline values significantly reduced Didymo biomass during both experiments, though the P enrichment effect diminished with distance downstream. Findings by James al. (2015) supported the hypothesis that Didymo blooms are driven by P limitation.

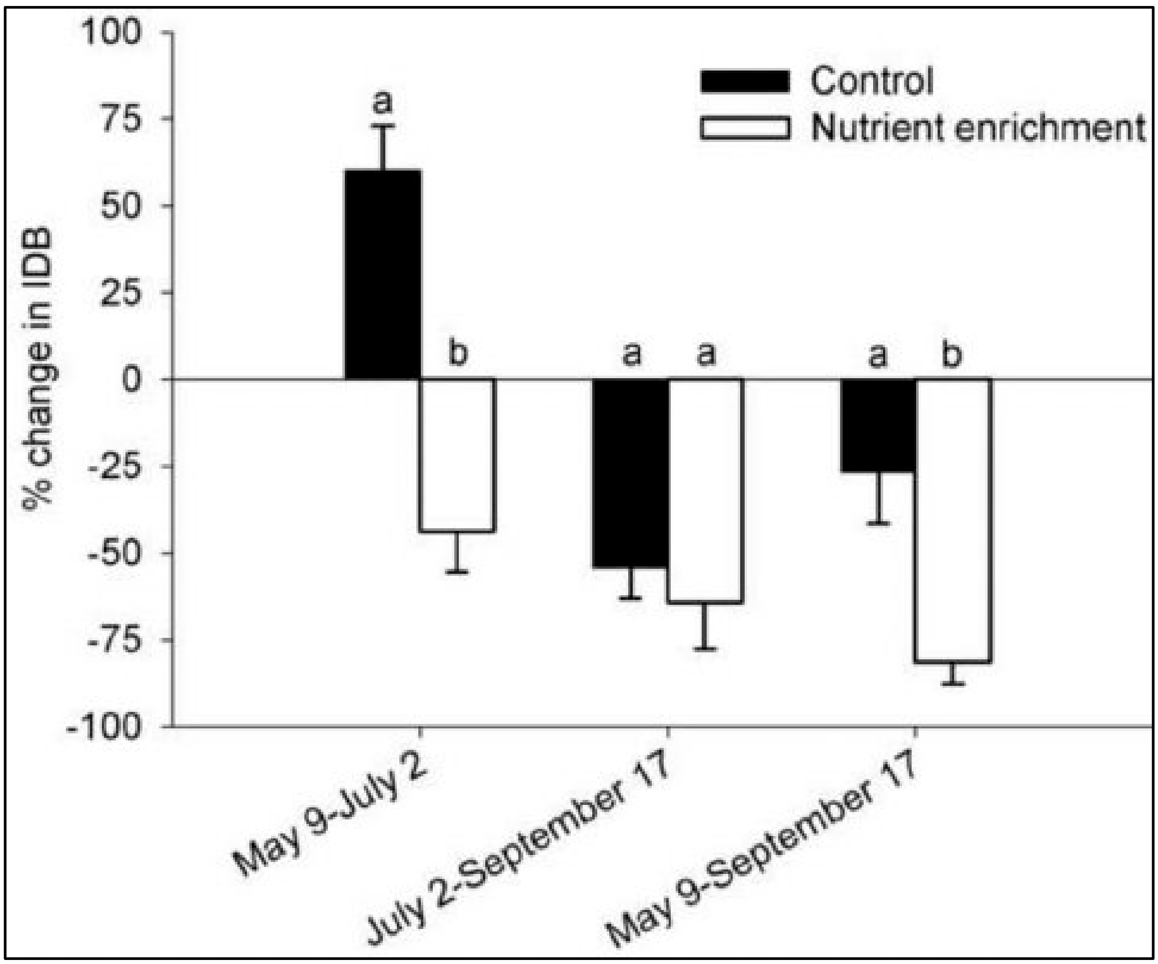

Figure from James et al. 2015. "Mean (+1 SE; n = 4 for each occurrence) relative change in the index of *Didymosphenia geminata* biomass (IDB), expressed as the % change from one sampling date to the next at control and nutrient-enrichment sites in Rapid Creek, South Dakota, during 2007. Bars with the same letters (within times) are not significantly different (t -test). "

James, D. A., and S. R. Chipps. 2016. Influence of *Didymosphenia geminata* Blooms on Prey Composition and Associated Diet and Growth of Brown Trout. Transactions of the American Fisheries Society 145:195-205.

As a companion to their phosphorous enrichment experiments (James et al. 2015), James and Chipps (2016) examined the effects of Didymo on the diet, fullness, condition, and growth of Brown Trout with and without Didymo blooms. Their study area included one reach in each of three streams in the Black Hills of South Dakota. Comparison of diet composition, stomach fullness, relative weight, and growth of Brown Trout between the one stream with and two streams without Didymo blooms revealed similarities and differences. For example, Ephemeroptera were less abundant in the stream with Didymo blooms than in the streams without Didymo blooms, and Ephemeroptera were a smaller component of small Brown Trout diets in the stream with than streams without blooms. Neither availability nor consumption of Plectopera and Trichoptera differed among streams. Diptera (e.g., midges) were more abundant in the stream impacted by Didymo than in the streams not impacted by Didymo, but Brown Trout diets did not mirror that contrast. Stomachs of small Brown Trout were fuller in the Didymo-affected stream, whereas, fullness of large Brown Trout was comparable among streams. Relative weight of large Brown Trout was highest in the stream with Didymo blooms, but relative weight of small Brown Trout was similar among streams. No contrast was observed between the biomass of Brown Trout in the one stream with and two streams without blooms. Comparison of length-at-age data from one stream with and one stream without Didymo revealed no differences in size at ages 1 or 2, but a significant difference at age 3—namely, total length of Age-3 Brown Trout was greater in the Didymo-affected stream. James et al. (2016) concluded that, in light of their findings and those from other studies in the past, Didymo might not have an obvious, deleterious effect on small trout.

Table reproduction using data from James and Chipps (2016). Comparison of Brown Trout biomass (mean ± SE) from one stream with and two streams without Didymo blooms (TL = total length). Superscript Letters (e.g., ^{a}) denote statistically significant differences or lack thereof at $\alpha = 0.05$ (same letter = no significant difference).

Biomass (kg/ha)		
With Didymo blooms	Without Didymo blooms	
Small Brown Trout (TL: 100-199 mm)		
118.7 ± 18.1^{a}	9.7 ± 2.1^{b}	130.3 ± 13.1^{a}
Large Brown Trout (TL 200-300 mm)		
34.2 ± 6.2^{a}	34.6 ± 9.5^{a}	94.3 ± 10.8^{a}

Jellyman, P. G., and J. S. Harding. 2016. Disentangling the stream community impacts of *Didymosphenia geminata*: How are higher trophic levels affected? Biological Invasions 18:3419-3435.

Jellyman and Harding (2016) collected data from 20 streams in southern New Zealand, where Didymo had been introduced, and used a variety of analytical techniques to test a number of hypotheses regarding drivers of and trophic web responses to Didymo blooms. Overall, their results suggested that Didymo biomass increased with time elapsed since the last major flow event (discharge > 3x median flow) and decreased with dissolved reactive phosphorous concentration (especially below 4 ppb). Further, results suggested that Didymo had generally positive effects on benthic and drifting invertebrates, with trickle-down positive effects on fish. For example, Didymo biomass was positively associated with total invertebrate density (but negatively associated with density and proportion of EPT taxa [mayflies, stoneflies and caddisflies]). Nevertheless, the authors found that indirect positive effects of Didymo on fish were outweighed by the combination of direct and indirect negative effects on fish. Moreover, Didymo biomass was inversely related to trout biomass, the former explaining 30% of the variation in the latter. Jellyman and Harding (2016) concluded that indirect effects of Didymo on fish—for example, reduced availability of EPT—were ultimately less influential than unidentified direct effects.

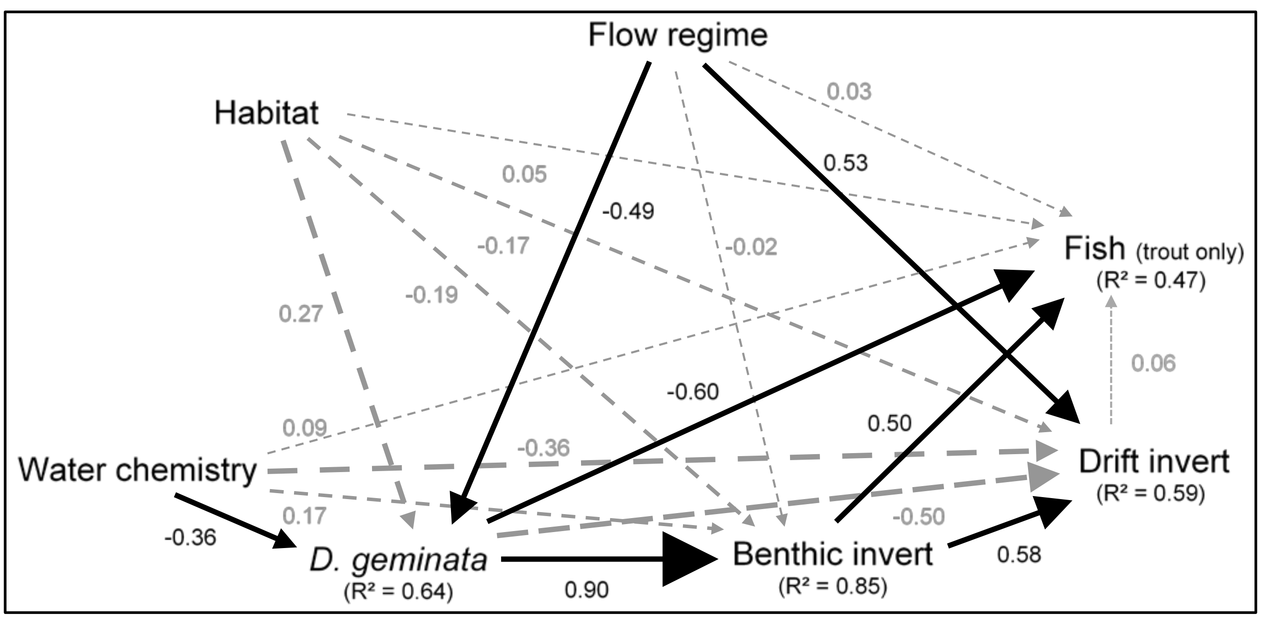

Figure from Jellyman and Harding 2016 (and supporting information). "PLS path diagram used to assess both direct and indirect effects on fish communities. Arrows point from predictor to response variables within the model and the thickness of the arrows are proportional to the respective path values (mean bootstrapped standardised path coefficients). Solid black lines indicate significant effects and dashed grey lines indicate non-significant effects as determined from the bootstrapping procedure. Coefficients of determination (R 2) are reported for response variables within the model."

Bothwell, M. L. and B. W. Taylor. 2017. Blooms of benthic diatoms in phosphorous-poor streams. Frontiers in Ecology 110-111.

In their brief note, Bothwell and Taylor (2017) explained the seemingly paradoxical relationship between nutrients and Didymo. The authors explained that in a phosphorous-poor stream, Didymo undergoes relatively slow cell division, which results in stalk elongation and development of a visible mat. Conversely, in a phosphorous-rich stream, Didymo undergoes rapid cell division, which results in development of short, less-visible stalks. Bothwell and Taylor (2017) noted that, in the case of Didymo, mat formation and increased visibility does not necessarily equate to increased biomass.

Kunza, L. A., C-A Gillis, J. Z. Haueter, J. N. Murdock, and J. M. O'Brien. 2018. Declining phosphorous as a potential driver for the onset of *Didymosphenia geminata* mats in North American rivers. River Research and Applications 34(8):1105-1110.

Kunza and others (2018) opened their paper by articulating two common hypotheses for the rapid, worldwide increase of Didymo blooms: 1) widespread introduction of Didymo to previously unoccupied waters and 2) response by pre-existing Didymo populations to changes in environmental conditions. Further, they noted that studies on phosphorous limitation have supported both the environmental change hypothesis and the notion that phosphorous limitation is the most influential driver of Didymo blooms. The authors added, however, that evidence of environmental change preceding Didymo blooms is rare. To that end, they searched for North American datasets that included the initial bloom of pre-existing Didymo, a timeline for bloom formation, and a continuous record of phosphorous concentration. Datasets from only two rivers, the Kootenai and Matapedia, met the criteria. The authors also searched for evidence of Didymo blooms occurring in North American rivers where the soluble reactive phosphorous (SRP) concentration was higher than the hypothesized trigger point of 2 ppb. Kunza et al. (2018) found several examples of Didymo blooms occurring at SRP concentrations > 2 ppb, but none at SRP concentrations > 12 ppb. In both the Kootenai and Matapedia rivers, general declines in phosphorous availability preceded the onset of Didymo mat formation (i.e., Didymo blooms). However, in the Kootenai River, the first Didymo bloom occurred approximately 20 years after the SRP concentration dropped below 2 ppb (25 years after SRP dropped below 12 ppb) and, in the Matapedia River, the first Didymo bloom occurred approximately two years after the SRP concentration fell below 10 ppb. The authors concluded that, while the overall decline in available phosphorous might have favored Didymo blooms, the lag time between the crossing of a hypothesized SRP threshold and the onset of blooms suggests other environmental factors might exist.

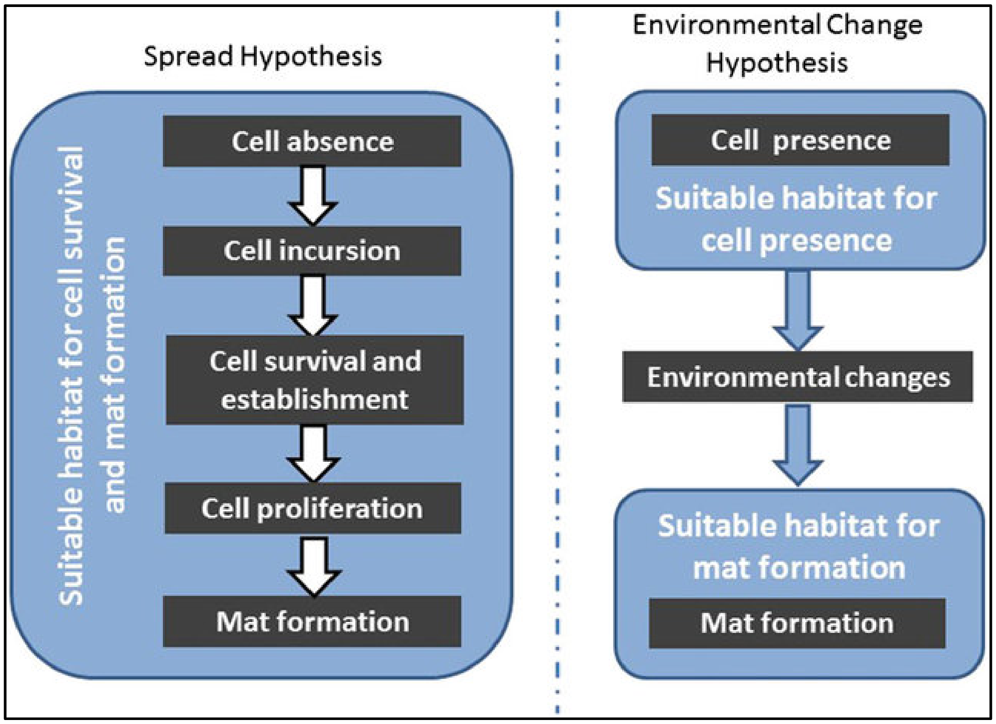

Figure from Kunza et al. (2018). **"**Conceptual diagram of the two competing hypotheses for the increasing occurrence of *D. geminata* mats in rivers worldwide."

Clancy, N. G., J. Brahney, J. Dunnigan, and P. Budy. 2021. Effects of a diatom ecosystem engineer (*Didymosphenia geminata*) on stream food webs: implications for native fishes. Canadian Journal of Fisheries and Aquatic Sciences 78(2):154-164.

Clancy et al. (2021) used two methods of study to examine the relationships among Didymo, benthic macroinvertebrates, and coldwater fishes (trout [*Oncorhynchus* spp.], char [*Salvelinus* spp.], and sculpin [*Uranidea* spp.]). The first method consisted of a mechanistic study, wherein the authors compared invertebrate- and fish-related metrics between streams with and without Didymo. The second method consisted of a multi-stream study, wherein the authors examined invertebrates and fish across a gradient of Didymo streambed coverage. During the June-August period of the mechanistic study, EPT (mayflies, stoneflies, caddisflies) taxa were more common drift items in the stream without Didymo whereas Dipterans (e.g., midges) were more common drift items in the stream with Didymo. Nevertheless, neither diet nor growth of trout appeared to differ. Trout were more abundant in the stream with Didymo than in the stream without, whereas the converse was true of total insect drift. During the observational study, the authors found no evidence of a relationship between Didymo coverage and condition of trout and char, or of a relationship between Didymo coverage and fish diet (except between % coverage and % aquatic prey among trout).

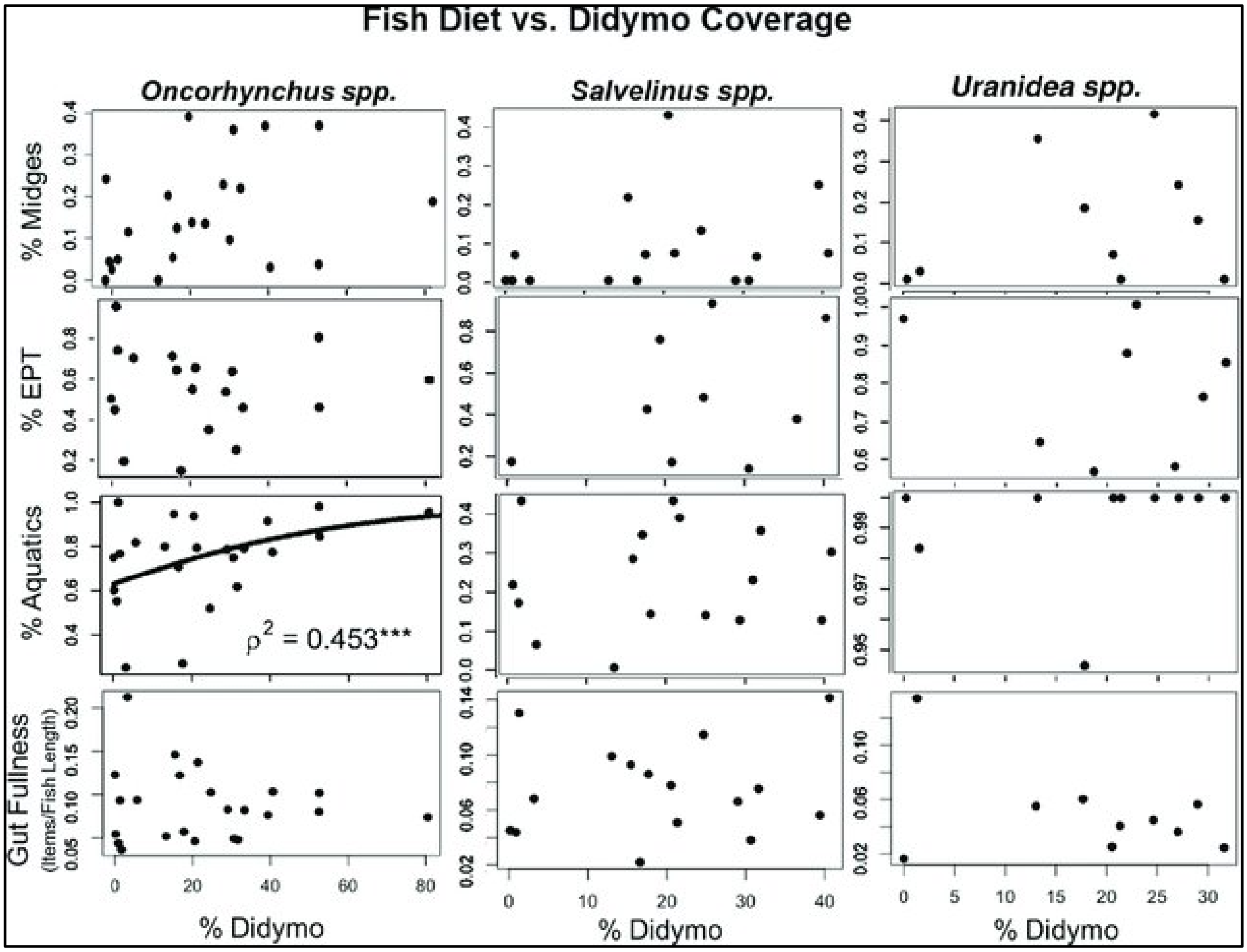

Figure from Clancy et al. (2021). **“**Correlations of Didymo coverage to each fish taxon's diet and condition response metrics from 2019. Each dot represents the average value for fish in a single stream. r 2 is Nagelkerke's pseudo-R 2 value. Asterisks (***) indicate p ≤ 0.05. Results indicate few relationships between Didymo coverage and fish diet metrics.” Note: Oncorhynchus spp. = trout (including Redband Trout); Salvelinus spp. = Char (including Bull Trout); and Uranidea spp. = sculpin (including Columbia Slimy Sculpin).

Glossary

Benthic: associated with or occurring on the bottom.

Diptera: an order of insects including the "true flies" (e.g., flies, mosquitos, midges, and gnats).

Dissolved Reactive Phosphorous: commonly measured form of soluble phosphorus that is highly correlated with phosphorus availability for plant growth (orthophosphate); also called Soluble Reactive Phosphorous.

Ephemeroptera: an order of insects commonly known as mayflies

EPT (or EPT taxa): collectively, insects from orders Ephemeroptera, Plecoptera, and Trichoptera and commonly considered a indictor of water quality or environmental health.

Orthophosphate: mixture of orthophosphate ions $H_2PO_4^-$ and HPO_4^{2-}available to plants. Ratio of ionic forms dependent on pH. A mixture of both ions is typical in waters with pH 7-9.

Particulate Phosphorous: physical form of phosphorous consisting of phytoplankton, benthic algae, detrital algae, and other plant materials.

Plecoptera: an order of insects commonly known as stoneflies

Soluble Reactive Phosphorous: commonly measured form of dissolved phosphorus that is highly correlated with phosphorus availability for plant growth (orthophosphate); also called Dissolved Reactive Phosphorous.

Total Phosphorous: soluble reactive phosphorus (or dissolved reactive phosphorous) + particulate phosphorus.

Trichoptera: an order of insects commonly known as caddisflies