### FEATURE: INTRODUCED SPECIES

# On the Boots of Fishermen: The History of Didymo Blooms on Vancouver Island, British Columbia

ABSTRACT: In 1989 blooms of the river benthic diatom Didymosphenia

geminata (didymo) first appeared and rapidly spread among rivers on central Vancouver Island, covering the bottoms with thick, woolly-looking mats. Although didymo is native to North America, extensive field surveys of rivers on Vancouver Island and other data indicate that didymo blooms are new. No known environmental changes were associated with the onset of didymo blooms. However the pattern of didymo spread among rivers on Vancouver Island correlates with the activity of fishermen and the commercial introduction and widespread use of felt-soled waders in the late 1980s. Since 1994 nuisance blooms of didymo have appeared in numerous other places in the Northern Hemisphere and South Island, New Zealand, all areas frequented by fishermen. Actions by government agencies to educate the public and restrict the use of felt-soled waders have been undertaken in some jurisdictions and at least one commercial manufacturer of waders will discontinue production of feltsoled models in the near future.

### En los Zapatos de los Pescadores: La Historia de los Afloramientos del Alga Didymo en la Isla de Vancouver, Columbia Británica

**RESUMEN:** En 1989 aparecieron por primera vez los afloramientos de la diatomea bentónica *Didymosphenia geminata* (didymo) y se extendieron rápidamente entre los ríos de la isla de Vancouver, cubriendo los fondos con manto grueso y difuso. Si bien didymo es un alga nativa de Norte de América, muestreos extensivos en los ríos de la isla de Vancouver y otros datos indican que los afloramientos de didymo son un fenómeno nuevo. Ningún cambio ambiental conocido se relaciona con el inicio de estos afloramientos. Sin embargo, el patrón de dispersión entre los ríos de la isla de Vancouver se correlaciona con la actividad pesquera y el uso extensivo de sobretodos con botas incluidas al final de la década de 1980. Desde 1994, los afloramientos nocivos de didymo han aparecido en muchos otros puntos del hemisferio norte, Isla del Sur y Nueva Zelanda, todas áreas frecuentadas por pescadores. Las agencias de gobierno han tomado acciones para educar al público y restringir el uso de sobretodos con botas en algunas jurisdicciones y en el futuro cercano, al menos una fábrica comercial de este tipo de vestimenta para la pesca descontinuará su producción.

Didymo covers rocks on the bottom of the Heber River, September 1989. Algal biomass greatly exceeded guidelines for protecting aquatic life in streams.

### Max L. Bothwell, Donovan R. Lynch, Harlan Wright, and John Deniseger

Bothwell is a research scientist with Environment Canada, Pacific Biological Station, Nanaimo, British Columbia, and is an adjunct professor in the Department of Biology, University of Victoria, Victoria, British Columbia. He can be contacted at max.bothwell@dfompo.gc.ca. Lynch is with Fisheries and Oceans at the Pacific Biological Station, Nanaimo. Wright was a senior technician at the British Columbia Conservation Foundation, Nanaimo, and is now with Ecofish Research Ltd., Courtenay, British Columbia. Deniseger is head of the Environmental Quality Section, British Columbia Ministry of Environment, Nanaimo.

### INTRODUCTION

Didymosphenia geminata (Lyngbye) M. Schmidt (didymo) is a freshwater benthic diatom historically described as inhabiting cold, nutrient-poor, clear water in montane and boreal streams and rivers. It grows attached to solid surfaces with polysaccharide stalks extruded from individual cells. The bifurcating division pattern of cells and associated stalks results in hemispherical colonies attached to stones. When growth conditions are favorable, colony expansion allows stalks to coalesce, forming thick, gelatinous masses that can smother pristine, rocky-bottomed rivers. These massive accumulations have caught the attention of biologists and alarmed fishermen by their noxious appearance and potential to degrade water quality and alter riverine food webs (Kilroy et al. 2006; Larned et al. 2007). Didymo has been dubbed "rock snot" in mass media coverage worldwide.

Early diatomists documented the distribution of *D. geminata* in circumboreal regions of Europe, Asia, and North America, leading to the assumption that it was native to cooler, pristine waters in many parts of the Northern Hemisphere (Blanco and Ector 2009). While much of the early scientific literature describing didymo is floristic, accounts of massive blooms of didymo cover-

ing Scandinavian river bottoms date back over a hundred years (Schmidt-Nielsen and Printz 1915; Skulberg 1984; Lindstrom and Skulberg 2008). In North America, documented didymo blooms only began within the last 20 years (Bothwell and Spaulding 2008). The spread of didymo blooms between river systems in western and eastern regions of Canada and the United States, Iceland, Poland, Italy, Spain, and New Zealand has been alarming (Spaulding and Elwell 2007; Bothwell and Spaulding 2008; Blanco and Ector 2009). Didymo appears to be extending its range and is being found in climatic zones thought by ecologists to be outside its normal preferences, taking on the characteristics of an invasive species (Spaulding and Elwell 2007; Kumar et al. in press). Although *D. geminata* is native to British Columbia/Vancouver Island, there are cogent reasons to believe that didymo blooms in rivers on the island in the early 1990s were a new phenomenon. Expert witnesses of rivers on Vancouver Island in the years preceeding 1989 reported no unsightly algal blooms. Fisheries biologists working for the British Columbia Ministry of Environment (BC MoE) bear witness to the absence of didymo blooms in Vancouver Island rivers before 1989. Beginning in 1976, annual counts of steelhead escapement were made by the BC Fish and Wildlife Branch Steelhead Snorkel Survey Team (SSST), who wrote standardized reports following each survey. For 13 years, surveys were made without notable incident. However, in 1989 the SSST reported the

The first nuisance blooms didymo documented of North American rivers in occurred in British Columbia on Vancouver Island in the early 1990s (Sherbot and Bothwell 1993). All known contemporaneous (the past 20 years) didymo blooms in North America and elsewhere in the world followed the Vancouver Island episode, suggesting they might be causally related. We examined hydrological and water quality databases for possible factors that might have initiated didymo blooms on Vancouver Island. Several commonalities of didymo-infested rivers in British Columbia were identified, among which access by



The lower Gold River is typical habitat for didymo blooms on Vancouver Island in the early 1990s—broad, shallow, clear, rocky-bottomed river channels passing through forest corridors in remote areas popular with anglers.

the recreational public was prominent. Using British Columbia freshwater fishing license and steelhead tag data, we quantified public use of rivers by fishermen (angler days) and determined angler origin for major steelhead (*Oncorhynchus mykiss*) fishing streams on Vancouver Island. We compare the spread of didymo on Vancouver Island to outbreaks in other parts of the world and outline the efforts of government agencies and conservation organizations to inform aquatic recreational enthusiasts and professional river biologists about their probable role in the inadvertent spread of didymo both regionally and globally.

# DIDYMO ON VANCOUVER ISLAND, BRITISH COLUMBIA

#### Historical: pre-bloom era

Two of the earliest documentations of *Didymosphenia geminata* in North America are from British Columbia (Lord 1866; Cleve 1894-1896). In these early monographs, *D. geminata* is named by its synonym at the time, *Gomphonema geminatum*. Lord's samples came from the Columbia and Kootenay rivers in southern British Columbia while Cleve's sample was collected on Vancouver Island. Although the source of Cleve's specimen on Vancouver Island is not identified, we speculate that it might have been from the Cowichan River because it was a popular fly fishing river for Europeans in the late 1800s and *D. geminata* is common there today. bottom of the lower Heber River was completely covered in a blanket of didymo several centimeters thick. Having not seen it before, they did not know what it was (SSST members: L. Carswell, M. Lirette, F. Axford, and S. Rimmer, C. Wightman and R. Hooton, BC Fish and Wildlife Branch, Nanaimo, BC., pers. comms.). BC MoE biologists quickly identified didymo as the culprit.

Similarly, commencing in the early 1980s BC MoE environmental impact biologists conducted routine water quality assessments, which included algal biomass and community taxonomic measures, upstream and down-

stream of wastewater discharges into numerous Vancouver Island streams. Prior to 1988, *D. geminata* was not a significant contributor to the benthic algal community in any of the streams assessed, but in that year small patches of *D. geminata* first appeared and were identified in the Heber River near the confluence with the Gold River. By 1989, didymo mats covered 4 km of the lower Heber River.

The expert testimony that didymo blooms in rivers on Vancouver Island were a new phenomenon in the 1990s is also corroborated by data in a Canadian Department of Fisheries and Oceans scientific report published in 1985. Munro et al. (1985) quantified diatom species and abundance at multiple sites in the Puntledge River on Vancouver Island year round from 1978–1980. *D. geminata* was never sufficiently abundant to make the list of quantifiable diatom taxa, although it was occasionally present (Munro et al. 1985). Beginning in 1991 and continuing to present day, didymo blooms persist to varying degrees in the Puntledge River, where in some reaches it is often the dominant algal taxon. In sum, these reports provide objective evidence that didymo abundance in Vancouver Island's rivers prior to 1989 was low (i.e., non-bloom forming).

#### Bloom era: 1989-1994

Between 1989 and 1994, British Columbia Ministry of Environment biologists documented massive didymo blooms in 2 to 4 additional rivers each successive year, so that by 1994 persistent didymo blooms had been identified in 13 Vancouver Island watersheds (Figure 1). The BC MoE established the first website describing problematic blooms of didymo (www.env.gov.bc.ca/wat/wq/didy\_bcstrms. html).

River reaches infested with didymo on Vancouver Island in the early 1990s shared several characteristics. Blooms invariably appeared in the main stems of broad rockybottom river channels passing through forest corridors in unpopulated watersheds. The rivers were all clear, shallow, nutrientpoor streams with good exposure to sunlight (Sherbot and Bothwell 1993). While rivers with didymo often had headwater lakes or flow control structures, several did not (Table 1).

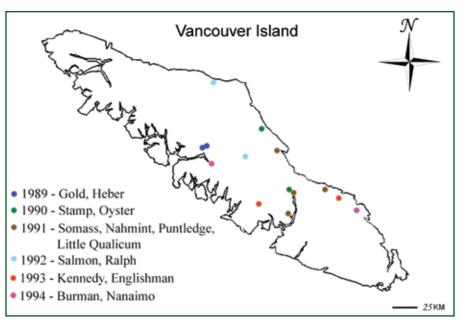
#### Post-bloom era: 1998-2008

After 1995, the spread of didymo blooms to new rivers on central Vancouver Island slowed. By 1998 the only major fishing river

added by the BC MoE to the list of didymo-affected rivers was the Cowichan River. More importantly, in the late 1990s didymo abundance began to wane in several of the rivers in which it had first bloomed 6 to 8 years previously. Didymo blooms in the Heber and Oyster rivers declined by 1998 and although didymo can be found in these rivers today, blooms have not been observed since circa 2000.

Notwithstanding the above, substantial mats of didymo still persist in limited reaches of Vancouver Island rivers downstream of flow control structures (e.g., the Puntledge, Little Qualicum, and Nanaimo rivers) and are especially prevalent along bedrock-bottom reaches. These observations corroborate that stabilized flows associated with lake outlets are preferred habitats for didymo and that stable substrata contribute to didymo persistence (Kawecka and Sanecki 2003; Kirkwood et al. 2007; Kirkwood et al. in press).

Figure 1. The rivers on Vancouver Island, British Columbia, Canada in 1989-1994 that were infested with didymo. The reaches of rivers impacted by didymo were all heavily accessed by the fishing and recreational public.



Although didymo is native to Vancouver Island, all evidence suggests that blooms starting in the 1990s were new events. The magnitude of blooms has substantially subsided in recent years, but the persistence of didymo in select habitats indicates that a lasting shift in algal communities on Vancouver Island has occurred.

# WHAT CAUSED DIDYMO BLOOMS ON VANCOUVER ISLAND?

#### The usual suspects

The causes of diatom blooms in rivers have been widely researched and are known to usually reflect changes in the chemical or physical characteristics of their habitat. Eutrophication (elevated nutrient levels) is the most frequently cited reason for excessive

> algal accumulations in rivers (Biggs 2000; Dodds et al. 2002). Diatom abundance in streams is also strongly affected by scouring events (Biggs and Close 1989). Selective shifts in diatom species composition, diversity, and abundance also reflect chemical and physical characteristics of their habitat (Stevenson and Pan 1999). We examined water chemistry and hydrological databases for rivers on Vancouver Island for possible clues as to what might have triggered the initial didymo blooms.

> The levels of soluble reactive phosphorus (SRP) in all didymo-affected rivers on Vancouver Island are extremely low, with mean values ranging from 2.2 to 4.4 ppb (Table 1), and have remained unchanged from the earliest samples in the 1970s to present day. These levels of SRP are typical for Vancouver Island streams and are in the low end of the expected range of North

Table 1. The chronology of the first didymo blooms and the primary characteristics of didymo-effected rivers on Vancouver Island between 1989–1994.
---

River	Year of first bloom	SRPª (µg/L)	Active steelhead fishery	Reservoir/Headwater Lake
Heber River	1989	2.2	Y	Ν
lower Gold River	1989	2.2	Y	Y
Stamp River	1990	3.6	Y	Y
Oyster River	1990	3.1	Y	Ν
Somass River	1991	3.2	Y	Y
Nahmint River	1991	NA	Y	Y
Puntledge River	1991	2.7	Y	Y
Little Qualicum River	1991	4.4	Y	Y
Salmon River	1992	NA	Y	Ν
Ralph River	1992	NA	Ν	Y
Kennedy River	1993	NA	Ν	Y
Englishman River	1993	2.3	Y	Y
Burman River	1994	NA	Y	Ν
Nanaimo River	1994	3.2	Y	Y

<sup>a</sup> Soluble reactive phosphorus; data from www.env.gov.bc.ca/emswr, values are the means. NA = data not available American rivers with forested catchments (Omernik 1977; Binkley et al. 2004). The presence of didymo blooms in nutrient-poor rivers corroborates the conclusion that didymo is an indicator of pristine water quality (Kirkwood et al. 2007). Although didymo responds positively to small amounts of enrichment, blooms of didymo are not initiated by eutrophication events (Kawecka and Sanecki 2003; Noga 2003; Bowman 2008).

In the years leading up to the didymo bloom era on Vancouver Island (1975-1988), the annual discharge of gauged rivers on central Vancouver Island varied widely but the temporal patterns were similar among rivers (Sherbot and Bothwell 1993). The years with lowest annual discharge and reduced winter scour events did not correspond with didymo blooms and there was no evidence that the outbreak of didymo on Vancouver Island was associated with a period of benign hydrological conditions (Sherbot and Bothwell 1993). In the absence of evidence that didymo blooms on Vancouver Island were a response to either changes in their chemical environment or physical forcing functions, we looked elsewhere. bed-smothering sediments, and substrata instability all seemed to play strong roles in determining those rivers that avoided didymo blooms.

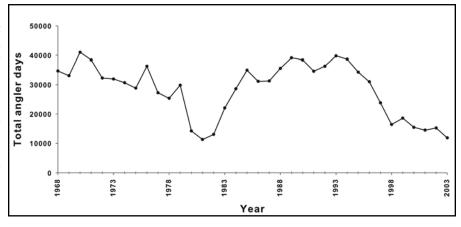
The British Columbia Steelhead Harvest Questionnaire database allowed us to quantify public use of many fishing streams on Vancouver Island and to evaluate the potential connection to the initiation and spread of didymo infestations. The total number of steelhead angler days each year fluctuated 4-fold between 1968 and 2003 with changes in steelhead returns and fishing regulations (Figure 2). Very low angler activity in 1980-1982 reflected the implementation of a catch-and-release fishery in response to declining steelhead stocks. However, beginning in 1983 and continuing for a decade, angler activity on Vancouver Island rivers rebounded dramatically following ramping up of the steelhead hatchery release program and a coincidental period of high ocean survival. Increased angler activity from 1983 into the 1990s was also seen on the Stamp River, where strong returns of hatchery-released steelhead allowed a greater catch-and-keep fishery (Figure 3). During this period of escalating fishing pressure, felt-

#### The probable role of fishermen

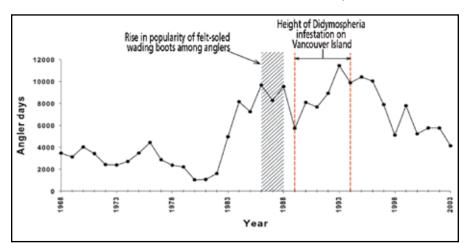
In addition to the physical and chemical commonalities of rivers supporting didymo blooms in the early 1990s on Vancouver Island, all but two were popular steelhead fishing sites (Table 1). The two exceptions were river sections immediately adjacent to either a popular campground (the Ralph River) or a highway rest stop (the Kennedy River), both heavily accessed by the public during summer months. Reaches of the Kennedy River just 3 km upstream of the public access point remained devoid of didymo in 1993. Furthermore, reaches of three rivers, the upper Gold River, the upper Salmon, and the upper Heber, that were prime didymo habitat did not support blooms in the 1990s. Records show that the upper Gold River and the upper Salmon were closed to fishing starting in 1982 and 1980, respectively. The upper Heber is not regularly fished because of a barrier to anadromous migration.

However, not all popular steelhead rivers on Vancouver Island or elsewhere in British Columbia succumbed to didymo blooms in the 1990s. Notable exceptions on the central part of the island were the Quinsam, Big Qualicum, and Campbell rivers that either had deep channels, heavy riparian shading, or mobile substrata. On northern Vancouver Island, the popular Keogh and Quatse rivers, both heavily stained with humate, did not support didymo blooms. The Dean River on the British Columbia mainland is a highly turbid river subjected to frequent spates of glacial flour. In spite of fishing pressure, the Dean also remained didymo-free. Reduced sunlight exposure from riparian shading and dissolved organic matter attenuation,

**Figure 2.** The total number of angler days for 12 steelhead rivers on Vancouver Island between 1968 and 2003. Data for the Heber, lower Gold, Stamp, Oyster, Somass, Nahmint, Puntledge, Little Qualicum, Salmon, Englishman, Burman, and Nanaimo rivers are summed. All of these rivers became didymo-effected in the early 1990s. The angler activity reflects changes in fishing regulations, size of the catch-and-keep hatchery stocks, and ocean survival. Data are from the British Columbia Provincial Fisheries Branch Steelhead Harvest Questionnaire database.



**Figure 3.** The number of angler days each year on the Stamp River from 1968 to 2003. Increased angler activity beginning in 1983 followed a ramping up of the hatchery release program and increased ocean survival of steelhead. Felt-soled waders and boots were commercially introduced in 1980s and were in wide use by 1988. Didymo blooms began on Vancouver Island in 1989. Angler data are from the British Columbia Provincial Fisheries Branch Steelhead Harvest Questionnaire database.



soled waders were commercially introduced and became widely popular in British Columbia by 1988 (Figure 3). Didymo blooms on Vancouver Island commenced shortly thereafter.

Studies in New Zealand have shown that retention of moisture in wader felts allows didymo cells to remain viable for many hours, even days, after leaving a river (Kilroy et al. 2007). As a vector for transport of didymo, wader felts may be the most problematic piece of fishing gear in wide use (Kilroy et al. 2007; Kilroy 2008). They have also recently been implicated in the spread of whirling disease (Gates et al. 2008) and New Zealand mudsnails (ANSTF 2007). Gates et al. demonstrated that the  $30+\mu m$  pore size of lightweight felts effectively retained mycospores of the parasite *Myxobolus cerebralis*, making wader felts a probable transmission vector for the disease.

### AN INVASIVE FORM OF GLOBALLY CIRCULATING DIDYMO?

The pattern and timing of didymo infestations among watersheds on Vancouver Island implicates fishermen in its regional movement, but it does not address the question of whether a bloom-forming variant of didymo might have been introduced to Vancouver Island. Angler-origin data from the British

Columbia steelhead tag program provides some insight. Coincidental with recovering steelhead fishing on Vancouver Island in the 1980s was the expansion of a commercial guided fishing industry. An apparent consequence of that development was an increase in the number of visitors from other parts of the world fishing rivers on the island. Between 1984 and 1990 the percentage of non-Canadians who fished for steelhead on Vancouver Island increased 3-fold from just 1% to more than 3%, a trend that continued to grow (Figure 4). The percentage of non-Canadians fishing for steelhead on mainland British Columbia rivers was even greater and steadily increased from 4-5% in the 1970s to 14% by 2000 (Figure 5). Such shifts in demography of fishermen could significantly elevate the risk of trans-national movement of nuisance aquatic microorganisms and the increased global mobility of fishermen may be the basis for the rapid-fire spread of didymo internationally.

Closely following the infestations on Vancouver Island, nuisance blooms of didymo began to be reported in other parts of the world. They first appeared in Iceland in 1994 (Jonsson et al. 2000). Didymo had not been recorded in Iceland previously and blooms spread rapidly to other rivers on the island nation by 1997. No apparent relationship was found among those rivers with didymo except that all were popular Atlantic salmon (*Salmo salar*) fishing rivers. In a nearly identical scenario to the Vancouver Island experience, didymo blooms have since waned in many Icelandic rivers while persisting in others (Jonsson et al. 2008). The pattern of didymo blooms suddenly appearing where none existed previously, followed by an equally sudden collapse a few years later, is classic behavior for populations of invasive species (Simberloff and Gibbons 2004). This supports the suggestion that although didymo is native to broad geographic regions, one or more variants of didymo may be being transported globally (Bothwell and Spaulding 2008; Blanco and Ector 2009; Spaulding et al. in press).

Other infestations of didymo within the past 10 to 15 years also highlight the likely connection to globally-mobile fishermen. Best known of these is the appearance of didymo in the lower Waiau River, Southland, New Zealand, in October 2004 (Kilroy 2004). In this instance didymo was almost certainly introduced by humans and in the past four years has spread to 26 catchments on South Island (Kilroy 2008; Spaulding et al. in press). Although all forms of recreational river use are potential vectors for transport of didymo, the river sites of most early infestations on New Zealand's South Island are highly accessed by trout fishermen (Kilroy 2008).

In North America several regional instances of didymo blooms have been associated with well-known salmonid fishing streams since the Vancouver Island episode of the early 1990s. Didymo

**Figure 4.** The percent of steelhead anglers fishing rivers on Vancouver Island between 1984 and 2000 that were not Canadian residents. The guided fishing tour industry expanded on Vancouver Island in the 1980s resulting in a greater percentage of non-Canadian fishermen. Data are from the British Columbia Provincial Fisheries Branch Steelhead Harvest Questionnaire database.

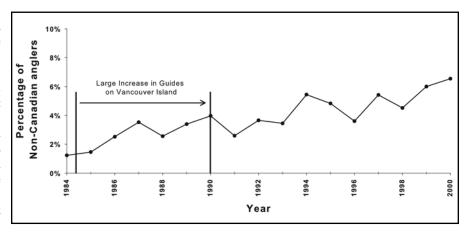
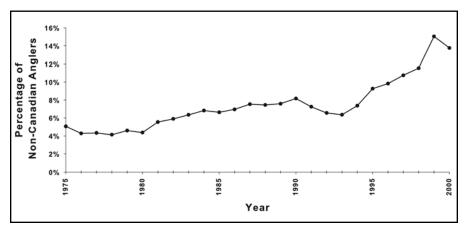


Figure 5. The percent of steelhead anglers fishing all rivers in British Columbia between 1975 and 2000 that were not Canadian residents. Data are from the British Columbia Provincial Fisheries Branch Steelhead Harvest Questionnaire database.



Fisheries • VOL 34 NO 8 • AUGUST 2009 • WWW.FISHERIES.ORG

blooms appeared in Rapid Creek, South Dakota, downstream of the Pactola Reservoir in 2002. Ten kilometers of river were heavily impacted, coinciding with a dramatic decline in the blueribbon brown trout (*Salmo trutta*) fishery (Shearer and Erickson 2006; Larson and Carriero 2008). In 2006 didymo blooms were first reported in the Atlantic salmon fishing reaches of the Matapédia River in Quebec and have since spread to other rivers in the lower St. Lawrence region, the Gaspe Peninsula, and adjacent New England states (Simard and Simoneau 2008).

### WHAT IS BEING DONE?

All of the evidence suggesting that recreational fishermen have played a role in the movement of didymo regionally and globally is circumstantial. However, there are now multiple lines of such evidence from around the world supporting this view, building a compelling case for action. Government agencies have been involved in public awareness campaigns. Biosecurity New Zealand provided the leadership in developing and publishing protocols for cleaning river fishing gear of didymo (www.biosecurity.govt.nz/pests/didymo/cleaning-specific#felt). These precautions have been widely publicized in North America (www.epa. gov/region8/water/didymosphenia/). Two Canadian provinces (New Brunswick and Quebec) have didymo awareness programs (www.gnb.ca/0254/FAQDidymo-e.asp; www.mddep.gouv.qc.ca/ biodiversite/eae/didymo.htm) and Parks Canada will begin issuing didymo-alerts to purchasers of freshwater fishing licenses in 2009 (G. Scrimgeour, Parks Canada, Calgary, Alberta, pers. comm.). Workshops sponsored by the Federation of Fly Fishers and the U.S. Environmental Protection Agency in Bozeman, Montana, in 2006 and by the Atlantic Salmon Federation and Environment Canada in Montreal in 2007, have helped inform academics and governmental and non-governmental agencies about didymo (Spaulding and Elwell 2007; Bothwell and Spaulding 2008). In combination with coverage in the popular press, this publicity has resulted in didymo being added to the global invasive species list by the United Nations Global Invasive Species Programme and the Northeast Aquatic Nuisance Species Panel. The combined concerns of biologists and conservation and fisheries agencies have led industry to search for alternatives to felt-soled boots and one manufacturer has announced that they will discontinue feltsoled models in 2010.

As of October 2008, New Zealand has banned the use of footwear with felt soles by fishing licence holders, but fishermen are not the only ones using rivers. Academic and government scientists, aquatic biologists, and water quality and hydrometric monitoring personnel wade rivers frequently in the conduct of their jobs. In North America, few of these agencies take the systematic precautions needed to prevent the spread of aquatic invasive microorganisms such as didymo. However, the U.S. Fish and Wildlife Service recently adopted a new policy (www/fws.gov/ policy/750fw1.html) to help prevent the spread of invasive species in its Fisheries Program operations through the use of Hazard Analysis and Critical Control Points planning. The Canadian Rivers Institute has also adopted protocols for field parties requiring the decontamination of footwear when moving between rivers (J. Culp, University of New Brunswick, Fredericton, New Brunswick, pers. comm.) We hope these proactive measures will be followed by other government agencies.

#### ACKNOWLEDGEMENTS

Sue Billings, British Columbia Fish and Wildlife Branch, Victoria, provided the analysis of visiting angler days for Vancouver Island streams. M. McCulloch and R. Hooton, British Columbia Fish and Wildlife Branch, Nanaimo, provided historical records of fishing closures and angler numbers. R. Nordin provided numerous reports (published and unpublished) of early didymo observations on Vancouver Island and J. Etzkorn assisted with figure production.

#### REFERENCES

- ANSTF (Aquatic Nuisance Species Task Force). 2007. National management and control plan for the New Zealand mudsnail (*Potamopyrgus antipodarum*). Available at: http://anstaskforce.gov/ Documents/NZMS\_MgmtControl\_Final.pdf.
- Biggs, B. J. F. 2000. Eutrophication of streams and rivers: dissolved nutrient-chlorophyll relationships for benthic algae. Journal of the North American Benthological Society 19:17-31.
- Biggs, B. J. F., and M. E. Close. 1989. Periphyton biomass dynamics in gravel bed rivers: the relative effects of flows and nutrients. Freshwater Biology 22:209-231.
- Binkley, D., G. G. Ice, J. Kaye, and C. A. Williams. 2004. Nitrogen and phosphorus concentrations in forest streams of the United States. Journal American Water Research Association 40:1277-1291.
- 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 Hegwigia 88: 347-422.
- Bothwell, M. L., and S. A. Spaulding. 2008. Synopsis of the 2007 International Workshop on *Didymosphenia geminata*. Pages xiiixxxi in M. L. Bothwell and S. A. Spaulding, eds. Proceedings of the 2007 International Workshop on *Didymosphenia geminata*, Montréal, Québec. Canadian Technical Report of Fisheries and Aquatic Sciences 2795.
- Bowman, M. F. 2008. Increased Didymosphenia geminata biomass in response to low-level phosphorus enrichment of oligotrophic rivers. Pages 30-31 in M. L. Bothwell and S. A. Spaulding, eds. Proceedings of the 2007 International Workshop on Didymosphenia geminata, Montréal, Québec. Canadian Technical Report of Fisheries and Aquatic Sciences 2795.
- Cleve, P. T. 1894-1896. Synopsis of the Naviculoid diatoms. Kongliga Sevenska Vetenskaps-Akademiens Handlingar. Stockholm. (Reprinted 1965, A. Asher and Co., Amsterdam).
- **Dodds, W. K., V. H. Smith,** and **K. Lohman.** 2002. Nitrogen and phosphorus relationships to benthic algal biomass in temperate streams. Canadian Journal of Fisheries and Aquatic Science 59:865-874.
- Gates, K. K., C. S. Guy, A. V. Zale, and T. B. Horton. 2008. Adherence of Myxobolus cerebralis myxospores to waders: implications for disease dissemination. North American Journal of Fisheries Management 28:1453-1458.
- Jonsson, G. S., I. R. Jonsson, M. Bjornsson, and S. M. Einarsson. 2000. Using regionalization in mapping the distribution of the diatom species *Didymosphenia geminata* (Lyngbye) M. Schmidt in Icelandic rivers. Verhandlunge Internationale Vereinigung fur Theoretische und Angewandte Limnologie. 27:340-343.
- Jonsson, I. R., G. S. Jonsson, J. S. Olafsson, S. M. Einarsson, B T. Antonsson. 2008. Occurrence and colonization pattern of Didymosphenia geminata in Icelandic streams. Pages 41-44 in M.

L. Bothwell and S. A. Spaulding, eds. Proceedings of the 2007 International Workshop on *Didymosphenia geminata*, Montréal, Québec. Canadian Technical Report of Fisheries and Aquatic Sciences 2795.

- Kawecka, B., and J. Sanecki. 2003. *Didymosphenia geminata* in running waters of southern Poland – symptoms of change in water quality? Hydrobiologia 495:193-201.
- Kilroy, C. 2004. A new alien diatom *Didymosphenia geminata* (Lyngbye) Schmidt: its biology, distribution, effects and potential risks for New Zealand fresh waters. National Institute of Water and Atmospheric Research Client Report CHC2004-128. Christchurch, New Zealand.
- 2008. Didymosphenia geminata in New Zealand: Distribution, dispersion and ecology of a non-indigenous invasive species. Pages 15-20 in M. L. Bothwell and S. A. Spaulding, eds. Proceedings of the 2007 International Workshop on *Didymosphenia geminata*, Montréal, Québec. Canadian Technical Report of Fisheries and Aquatic Sciences 2795.
- Kilroy, C., B. Biggs, N. Blair, P. Lambert, B. Jarvie, K. Dey, K. Robinson, and D. Smale. 2006. Ecological studies on *Didymosphenia geminata*. National Institute of Water and Atmospheric Research Client Report: CHC2005-123. Christchurch, New Zealand.
- Kilroy, C., A. Lagerstedt, A. Davey, and K. Robinson. 2007. Studies on the survivability of the exotic, invasive diatom *Didymosphenia geminata* under a range of environmental and chemical conditions. National Institute of Water and Atmospheric Research Client Report: CHC2006-116. Christchurch, New Zealand.
- Kirkwood, A. E., T. Shea, L. J. Jackson, and E. McCauley. 2007. Didymosphenia geminata in two Alberta headwater rivers: an emerging invasive species that challenges conventional views on algal bloom development. Canadian Journal of Fisheries and Aquatic Science 64:1703-1709.
- Kirkwood, A. E., L. J. Jackson, and E. McCauley. In press. Are dams hotspots for *Didymosphenia geminata* blooms? Freshwater Biology: in press, DOI: 10.1111/j.1365-2427.2009.02231.x
- Kumar, S., S. A. Spaulding, T. J. Stohlgren, K. A. Hermann, T. S. Schmidt, and L. L. Bahls. In press. Potential habitat distribution for the freshwater diatom *Didymosphenia geminata* in the continental US. Frontiers in Ecology and the Environment 7: in press, DOI: 10.1890/080054.
- Larned, S., D. Arscott, N. Blair, B. Jarvie, D. Jellyman, K. Lister, M. Schallenberg, S. Sutherland, K. Vopel, and B. Wilcock. 2007. Ecological studies of *Didymosphenia geminata* in New Zealand, 2006-2007. National Institute of Water and Atmospheric Research Client Report: CHC2007-050. Christchurch, New Zealand.
- Larson, A. M., and J. Carriero. 2008. Relationship between nuisance blooms of *Didymosphenia geminata* and measures of aquatic community composition in Rapid Creek, South Dakota. Pages 45-49 in M. L. Bothwell and S. A. Spaulding, eds. Proceedings of the 2007 International Workshop on *Didymosphenia geminata*, Montréal, Québec. Canadian Technical Report of Fisheries and Aquatic Sciences 2795.
- Lindstrom, E.A., and O.M. Skulberg. 2008. *Didymosphenia geminata*—a native diatom species of Norwegian rivers coexisting with the Atlantic salmon. Pages 35-40 *in* M. L. Bothwell and S.A. Spaulding, eds. Proceedings of the 2007 International Workshop on *Didymosphenia geminata*, Montréal, Québec. Canadian Technical Report of Fisheries and Aquatic Sciences 2795.
- Lord, J. K. 1866. Naturalist in Vancouver Island and British Columbia. Vols. 1, 2. R. Bentley. Spottiswoode and New-Street Square, London.

- Munro, K. A., S. C. Samis, and M. D. Nassichuk. 1985. The effects of hatchery effluents on water chemistry, periphyton and benthic invertebrates of selected British Columbia streams. Canadian Manuscript Report of Fisheries and Aquatic Sciences 1830: xvii +203p.
- **Noga, T.** 2003. Dispersion of *Didymosphenia geminata* in the flowing waters of southern Poland—new sites of species occurrence in the Orawska Watershed and the Orawska Basin. Oceanological and Hydrobiological Studies 32:159-170.
- Omerick, J. M. 1977. Nonpoint source-stream nutrient level relationships: a nationwide study. Special Studies Branch Corvallis Environmental Protection Laboratory. Office of Research and Development, U.S. Environmental Protection Agency. EPA-600/3-77-105.
- Schmidt-Nielsen, S., and H. Printz. 1915. Drammenselvens forurensning ved træmasse, cellulose- og papirfabrikkene 1911 og 1912. Biologiske og kjemiske undersøgelser, A. W. Brøggers boktrykkeri Kristiania: 142 pp.
- Shearer, J., and J. Erickson. 2006. Didymosphenia geminata and the Rapid Creek brown trout fishery, South Dakota. In American Fisheries Society Western Division Meeting, 15-16 May, 2006, Montana State University, Montana. Current knowledge of Didymosphenia geminata: developing a research and management response. Coordinated by S. Spaulding, R. Wiltshire, and L. Elwell. American Fisheries Society Western Division, Bozeman, Montana.
- Sherbot, D. M. J., and M. L. Bothwell. 1993. Didymosphenia geminata (Gomphonemaceae). A review of the ecology of *D. geminata* and the physiochemical characteristics of endemic catchments on Vancouver Island. NHRI Contribution 93005. National Hydrology Research Institute, Environment Canada, Saskatoon, Saskatchewan.
- Simard, I., and M. Simoneau. 2008. Didymo dans les rivières du Québec: état desituation. Pages 3-5 in M. L. Bothwell and S. A. Spaulding, eds. Proceedings of the 2007 International Workshop on *Didymosphenia geminata*, Montréal, Québec. Canadian Technical Report of Fisheries and Aquatic Sciences 2795.
- Simberloff, D., and L. Gibbons. 2004. Now you see them, now you don't—population crashes of established introduced species. Biological Invasions 6:161-172.
- Skulberg, O. M. 1984. Effects of stream regulation on algal vegetation. Pages 107-124 *in* A. Lillehammer and S. J. Saltveit, eds. Regulated rivers. Columbia University Press, New York.
- **Spaulding, S. A.,** and **L. Elwell.** 2007. Increase in nuisance blooms and geographic expansion of the freshwater diatom *Didymosphenia geminata:* recommendations for response. USGS Open File Report 2007-1425.
- Spaulding, S. A., C. Kilroy, and M. B. Edlund. In press. Diatoms as nonnative species. *In* J. P. Smol and E. F. Stoermer, eds. The diatoms: applications for the environmental and earth sciences. Cambridge University Press, UK.
- Stevenson, R. J., and Y. Pan. 1999. Assessing environmental conditions in rivers and streams with diatoms. Pages 11-40 in E.F. Stoermer and J. P. Smol, eds. The diatoms: applications for the environmental and earth sciences. Cambridge University Press, UK.