

Distribution, ecology and nuisance effects of the freshwater invasive diatom *Didymosphenia geminata* (Lyngbye)

M. Schmidt: a literature review

by

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With 5 figures

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Abstract: The diatom *Didymosphenia geminata* (Lyngbye) M. Schmidt has been commonly considered a taxon restricted to pristine habitats in mountainous areas of circumboreal regions. Recent studies show that it has a broader distribution and ecological amplitude. This shift seems to have occurred recently, as it now forms large growths in rivers within its native geographical area (North America, Europe) but also mass developments have recently appeared in New Zealand, where it is considered an aggressive invasive species with dramatic ecological and economic impacts. This nuisance organism grows attached in streambeds and may impact freshwater fish and aquatic plants and insects, causing severe disturbance in food webs. This paper investigates the historic and current biogeographic range of this invasive species (and varieties) based on 1000 citations collected mainly from the scientific literature. The locations where this diatom has appeared, including both fossil and recent records, are presented in world distribution maps. Our results confirm that the native range of *D. geminata* is almost restricted to the Holarctic region, though its distribution area is broader than usually reported in the literature. The ecological profile of this alga, along with its nuisance effects, is also discussed. Excessive growths do not only appear in areas where this species is presumably exotic. Contrarily to general statement, reports of mass developments of *D. geminata* date back to the 19th century. World references to *D. geminata* have increased exponentially during the last decades; however, with respect to the whole diatom literature during the XIX and XX centuries, the relative frequency of citations has decreased progressively.

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Introduction

Historically, the concept of invasive algae has been restricted to marine environments, where the ecological impacts of species such as *Caulerpa taxifolia* (Vahl) C.Agardh, *Codium fragile* (Suringar) Hariot or *Sargassum muticum* (Yendo) Fensholt are relatively well known. On the contrary, microalgae such as freshwater diatoms have been considered traditionally as cosmopolitan organisms (e.g. Finlay 2002); however, this paradigm has been questioned in several recent studies (Kociolek & Spaulding 2000, Hillebrand et al. 2001, Foissner 2006, Kilroy et al. 2007). The distribution and progression of selected taxa were investigated by Coste & Ector (2000) who revealed the presence of new diatom species for the European flora, some of them found in large populations in certain locations. Due to their fast proliferation in non-native habitats, often displacing indigenous taxa, most of them can be considered as invasives.

Nowadays there exists an increasing concern about the recent dispersal and negative environmental effects of the freshwater diatom alga *Didymosphenia geminata* (Lyngbye) M.Schmidt in A.Schmidt 1899, which is currently acknowledged as one of the most harmful invasive organisms in lotic systems worldwide (Sherbot & Bothwell 1993, Beltrami et al. 2008a, b, c, Pederson & Blakeslee 2008). *Didymosphenia geminata* is forming excessive growths in many streams and rivers of North America, New Zealand and Europe (Kilroy 2004a, b). In these areas this alga is expanding its geographical range and forming massive growths in streams and channels. *Didymosphenia* grows attached in streambeds and may impact freshwater fish and aquatic plants and insects, causing severe disturbance in food webs (Shelby 2006a, Marshall 2008). *Didymosphenia geminata* is native to northern-latitude lakes and streams, and, according to the literature, it is considered to be restricted to low-nutrient, low-temperature habitats with little anthropogenic impact. However, in recent years, its distribution has changed; this diatom not only appears to be expanding its geographic area to lower latitudes and altitudes, but it increasingly forms extensive masses covering stream benthos (Spaulding et al. 2005a, b, Cary et al. 2007a, Bothwell & Spaulding 2008, Edlund et al. 2008). The situation seems to be especially critical in New Zealand and north-western USA. On the South Island of New Zealand, *Didymosphenia geminata* is an exotic introduced species that has been growing massively in several rivers and declared an “unwanted organism” by Biosecurity New Zealand (Kilroy et al. 2005a, OECD 2007).

Only few diatom taxa are known to form conspicuous growths in streams, e.g. *Cymbella janischii* (A.Schmidt) De Toni, *Gomphoneis eriense* (Grunow) Skvortsov in Skvortsov & K.I.Meyer, *G. herculeana* (Ehrenberg) Cleve, *G. minuta* (Stone) Kociolek et Stoermer (Bahls 2007a). *Gomphoneis minuta* relatively recently became a nuisance in French streams, a habitat where it is considered nonindigenous (Le Cohu & Coste 1995, Coste & Ector 2000, Stoermer & Andresen 2006). However, *D. geminata* is the first non-toxic benthic diatom known to cause strong negative effects on aquatic environments, though many aspects of its biology are still poorly understood. The main aim of this study is to assess the historic and recent distribution area of this species based on bibliographic records. We identify the ecological aspects underlying

its massive proliferation in several limnosystems worldwide. Furthermore, the study of the spatial-temporal distribution of this diatom provides indications of the causes leading to the geographic expansion of invasive microalgae.

Material and methods

In order to account for existing records of *D. geminata* worldwide, a near exhaustive investigation was performed in the scientific literature, phycological inventories, technical reports and internet databases. Where possible, the date of citation, along with the most accurate geographical location available, and ecological particularities were recorded. Data were analyzed and geo-referenced using GIS software. It must be noted that this bibliographic approach is affected by a triple bias: i) despite the fact that the diagnosis of *D. geminata* is relatively easy, even in untreated samples (Sterrenburg et al. 2007), in most cases the lack of iconographic material associated to the records, prevents the detection of taxonomic misidentifications, which are very likely present in technical reports and ancient works; ii) since phycological research effort varies among different world regions, biogeographical maps may reflect the distribution of floristic surveys rather than the actual distribution of a certain species; and iii) due to similar reasons, the comparison of modern and ancient distribution maps is not reliable. Nevertheless, because it is presumably the only feasible methodology, we use it to obtain a general view on the spatio-temporal distribution patterns of this species.

Results

Fourtanier & Kociolek (2008) identify the following nomenclatural synonyms of *D. geminata*: *Echinella geminata* Lyngbye, *Gomphonema geminatum* (Lyngbye) C.Agardh, *Styllaria geminata* (Lyngbye) Bory, *Dendrella geminata* (Lyngbye) Bory and *Lyngbyea pulvinata* var. *geminata* (Lyngbye) Sommerfelt. Unless otherwise stated, the taxonomic scope of the literature survey is limited hereafter to *Didymosphenia geminata* (Lyngbye) M.Schmidt sensu stricto, including: i) the emended (broadened) description of this taxon in Antoine & Benson-Evans (1984), ii) the nomenclatural synonyms, and iii) their validly published varieties and forms of *D. geminata* and its former nomenclatural synonyms, identified as such in the text. There are 26 taxa currently under this status:

- Didymosphenia geminata* var. *baicalensis* Skvortsov et K.I.Meyer
- D. geminata* var. *baicalensis* f. *capitata* Skvortsov et K.I.Meyer
- D. geminata* var. *baicalensis* f. *curta* Skvortsov et K.I.Meyer
- D. geminata* var. *baicalensis* f. *curvata* Skvortsov et K.I.Meyer
- D. geminata* var. *baicalensis* f. *elongata* Skvortsov et K.I.Meyer
- D. geminata* var. *curvata* f. *curta* Skvortsov et K.I.Meyer
- D. geminata* var. *curvata* f. *elongata* Skvortsov et K.I.Meyer
- D. geminata* var. *dorogostaiskii* Skvortsov et K.I.Meyer
- D. geminata* var. *dorogostaiskii* f. *curta* Skvortsov et K.I.Meyer
- D. geminata* var. *genuina* A.Cleve



Fig. 1: World distribution of fossil or subfossil records of *Didymosphenia geminata*. Black dots: *D. geminata* var. *geminata*. White dots: *D. geminata* var. pl. “?”: doubtful citation. Unspecified locations omitted.

- D. geminata* var. *genuina* f. *baicalensis* Skvortsov et K.I.Meyer
- D. geminata* var. *genuina* f. *curta* Skvortsov et K.I.Meyer
- D. geminata* var. *neocalledonica* Manguin
- D. geminata* var. *sibirica* f. *anomala* Skvortsov et K.I.Meyer
- D. geminata* var. *sibirica* f. *curta* Skvortsov et K.I.Meyer
- D. geminata* var. *sibirica* f. *curvata* Skvortsov
- D. geminata* var. *sibirica* f. *elongata* Skvortsov et K.I.Meyer
- D. geminata* var. *sibirica* f. *genuina* Skvortsov et K.I.Meyer
- D. geminata* var. *sibirica* f. *subcapitata* Skvortsov
- D. geminata* var. *stricta* M.Schmidt
- D. geminata* var. *stricta* f. *baicalensis* Skvortsov et K.I.Meyer
- D. geminata* var. *stricta* f. *capitata* Skvortsov et K.I.Meyer
- D. geminata* var. *stricta* f. *curvata* Skvortsov
- Gomphonema geminatum* var. *bipunctatum* Rattray
- G. geminatum* var. *curvatum* K.I.Meyer
- G. geminatum* var. *hybrida* Grunow
- G. geminatum* var. *norvegica* Holmboe

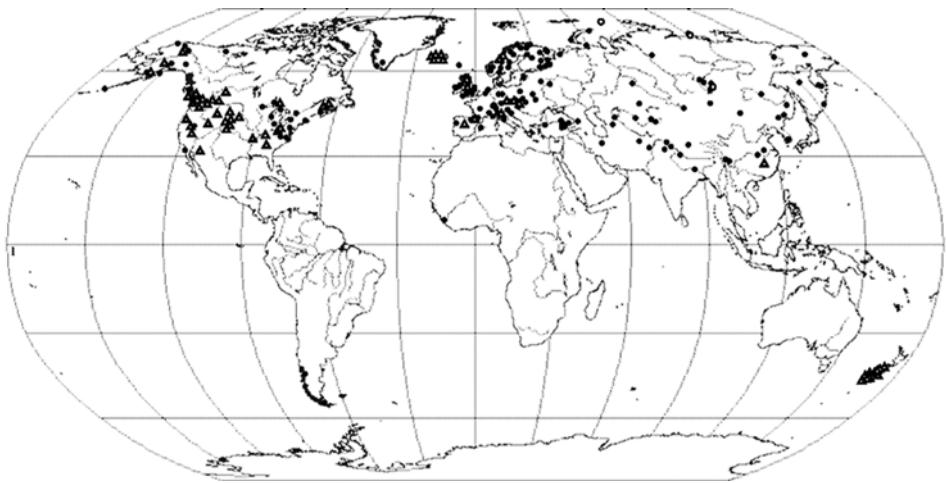


Fig. 2: World distribution of recent records of *Didymosphenia geminata*. Black dots: *D. geminata* var. *geminata*. White dots: *D. geminata* var. *pl.* Triangles: mass-forming *D. geminata* var. *geminata*. Unspecified locations omitted.

Up to 1000 references about *D. geminata* were found, from the description of this species, first discovered in the Faroe Islands by H.C.Lyngbye in 1817 (Lyngbye 1819), to 2008. Paleolimnological and recent records are presented arranged by countries and in chronological order. Also, records are plotted in biogeographical world maps (Figs 1 and 2). World references to *D. geminata* have increased exponentially during the last decades (Fig. 3); however, with respect to the whole diatom literature during the XIX and XX centuries (~145.000 references), the relative frequency of citations has decreased progressively (Fig. 4).

1. Fossil and subfossil records:

CANADA: Pierre Greys Lakes (Irish 1951), Lake O'Hara (H.Kling, pers. comm., 2007).

CHINA: Changbai and Hailong (Liu 1982), Fusong (Jiaying & Yuzao 1986).

FAROE ISLANDS: Skalafjord (Witon & Witkowski 2003).

FINLAND: Lapland (Hogg 1856), Kuolajärvi (Ramsay & Nyholm 1895), Outokumpu (Väyrynen 1939), Höytäinen, Humaljoki, Ino, Maaninka, Niemenkönkää (Cleve-Euler 1955), Otanmäki (Pääkkönen 1956), Lake Päijänne (Aario 1965), Baltic Sea (Snoeijns & Balashova 1998), Pohjanmaa (Eriksson et al. 1999), Iso Lehmälampi (Sarmaja-Korjonen & Alhonen 1999). Unspecified locations: Kivioja (1963), Haapala & Ojanperii (1972).

FRANCE: Cantal (Cleve 1894, Héribaud 1902).

GERMANY: Mecklenburg (Geinitz 1880).

INDIA: Lake Karewa (De Terra & Paterson 1939 [*G. geminatum* var. *hybrida*]), Baltal (Gandhi & Mohan 1983 [*G. geminatum* var. *hybrida*]).

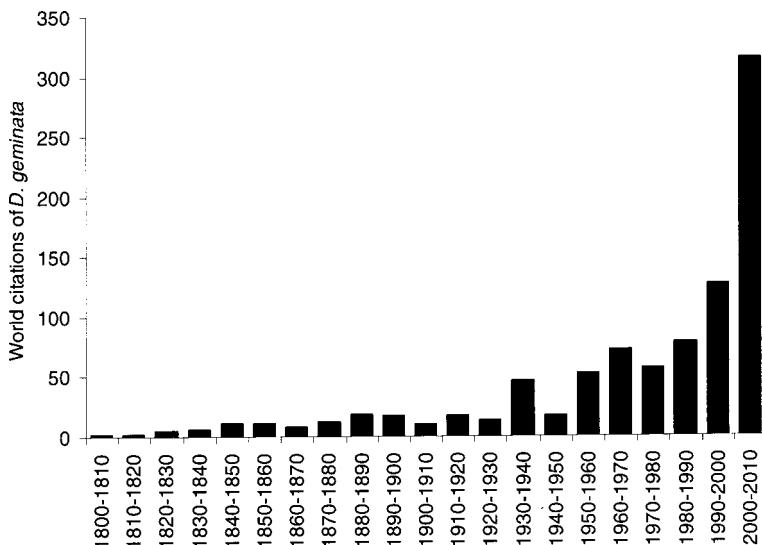


Fig. 3: World citations of *Didymosphenia geminata* in the scientific literature since 1800.

IRELAND: Lough Mourne (Ehrenberg 1842, Smith 1853).

ITALY: San Fiore, Tuscany (Mandl 1839, Pritchard 1842, Griffith & Henfrey 1883), Castelnovate, Lombardy (Corti 1893).

JAPAN: Onikoube Basin (Katayama 1955), Yatuka deposit (Tuji 2004).

MONGOLIA: Lake Hövsgöl (Dorofeyuk 1977), Lake Tsagan-Nur (Dorofeyuk 1984).

NORWAY: Stavanger (Héribaud 1902), Andøya (Foged 1978).

POLAND: Unspecified location: Marciniak & Przybyłowska-Lange (1977).

PORTUGAL: Central Portugal (Da Silva 1946).

RUSSIA: Lake Ladoga (Ailio 1915, Abramova et al. 1967, Davidova 1968), Pechenga (Väyrynen 1938), Yenisei River (Alyoshinskaya 1962, 1968, Skabichevskaya 1984), Lake Krasnoe (Vishnevskaya & Davidova 1963, Stanislavskaya 2007), Tighil River (Kozlova & Geptner 1965), Kamchatka River (Malaeva et al. 1965, Zaikina & Malayeva 1966, Zaikina & Lupikina 1968), Lake Baikal (Fedorova 1975 [incl. *D. geminata* var. *genuina*, *D. geminata* var. *genuina* f. *baicalensis*, *D. geminata* var. *genuina* f. *curta* and *D. geminata* var. *baicalensis*]), Edlund et al. 1995, Swann et al. 2006 [*D. geminata* var. *baicalensis* f. *curvata*], Laptev Sea (Cremer 1998, 1999), Lake Lama (Kienel 1999, Kienel & Melles 2000, Melles 2000, Kienel & Kumke 2002, Kienel et al. 2005), Kara Sea (Matthiessen et al. 1999, Polyakova & Stein 2004), Iturup Island (Razjigaeva et al. 2002), New Siberia Island (Olyunina 2004), Central Kola Peninsula (Olyunina 2005), Yakutia (Vasilyeva-Kralina et al. 2005), and Novosibirsk (Olyunina & Tumskoy 2006). Unspecified locations: Davidova (1985), Loseva (2000), Loseva et al. (2004).

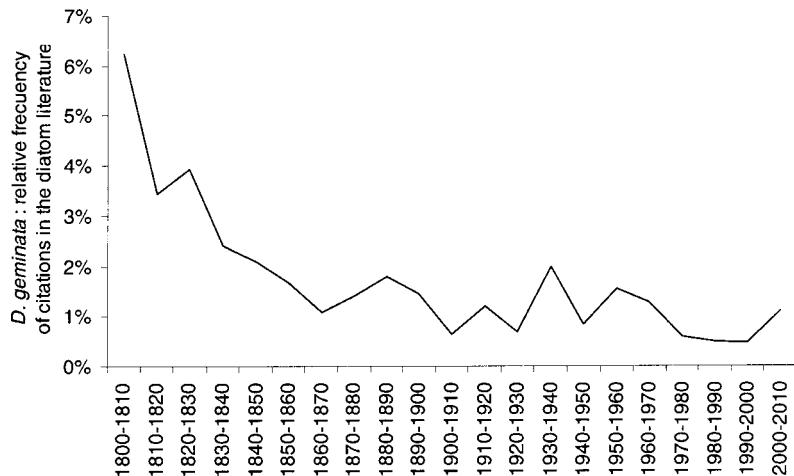


Fig. 4: Relative frequency (%) of citations of *Didymosphenia geminata* in the diatom literature since 1800.

SWEDEN: Ryssby (Holst 1888), Kalmar (Héribaud 1902), Lake Ancylus (Cleve-Euler 1911, 1944, 1955, Post 1915, Hustedt 1924, Hedenström & Risberg 1999), Abisko (Lundqvist 1939), Ådalen, Baltic Sea, Björnsjö, Erlången, Fågelvik, Galmeren, Grässjön, Härnö, Hornborgasjön, Järnlunden, Kristienhamn, Lule River, Ragunda, Roxen, Skattmansö, Strömsbro, Täflängen, Tanum (Cleve-Euler 1955), Ale (Fromm 1984), Söderköpenhamn Peninsula, Lake Svulten (Snoeijs & Balashova 1998). Unspecified locations in Norrland (Fagraeus 1890, Lundbohm 1899, Lundqvist 1936) and in Southern Sweden (Thunmark 1937).

UNITED KINGDOM: ENGLAND: Kentmere (Mitchell 1933), Lake Windermere (Jenkin et al. 1941, Pennington & Tutin 1943, Round 1957a, Sabater & Haworth 1995), Lakes Ennerdale, Derwentwater, Brother's Water, Bassenthwaite, Loweswater, Ullswater, Buttermere, Elterwater, Esthwaite Water, Grasmere (Round 1957a), Kentmere Valley (Round 1957b). SCOTLAND: Isle of Lewis (Rattray 1887 [*G. geminatum* var. *bipunctatum*]), Loch Leven (Haworth 1972), Loch Sionascaig (Pennington et al. 1972, Haworth 1976), and Loch Linton (Mannion 1978). WALES: Milford Haven (Okeden 1855). Unspecified locations: Paterson (1841), Queckett (1850), Johnston & Tate (1853).

UNITED STATES: Wildwood (Boyer 1895), Southern New Jersey (Woolman 1895), Long Island, New York (Lohman 1939), Amchitka Island (Gard 1980), Cache la Poudre River, Colorado (Oberholster 2005, Oberholster et al. 2005). Unspecified location in the Pacific Coast region (Mulryan 1939).

2. Distribution of recent records:

AFGHANISTAN: Panjshir (Foged 1959).

AUSTRIA: Enns River (Pfister 2002, Ács et al. 2003, Schiftner & Blatterer 2004), Steyr (Schiftner & Blatterer 2004), Lake in Kaernten, Carinthia (H.Ullrich, pers. comm., 2008). Unspecified locations: Rabenhorst (1864), Kann (1978).

BELARUS: Unspecified location: Mikheyeva (1999).

BELGIUM: Allain, Hainaut (Westendorp & Walleys 1844), Cortenberg (Conrad & Kufferath 1912). Unspecified location: Symoens (1950).

CANADA: Vancouver Island (Cleve 1894, Boyer 1927, Rieberger 1991, Sherbot & Bothwell 1993, Mundie & Crabtree 1997, Hansen 2003, Silvestri 2004), New Brunswick (Bailey 1910), Bay of Fundy (Bailey 1915), Island of Montreal (Miller 1915), Bathurst Inlet, St. John's Harbour (Bailey 1924), Sainte Annes (Lowe 1927), Lake Winnipeg (Bajkov 1934), Lake Kalamalka (Foerster 1936), Ontario (Duthie 1973), Yukon (Barracough 1992, YZC 2005, H.Kling, pers. comm., 2008), British Columbia (EVSEC 2004), Beaver Creek (Westcott et al. 2004), Columbia River (CRIEMP 2005), Attycelley Creek (Crippen 2005), Quebec (Bellavance 2006, Côté 2007, MDDEP-MRNF 2007, Blais 2008), Red Deer and Bow Rivers, Alberta (Elwell 2006, Kirkwood et al. 2007), Tsi-it-toh-Choh Range caves, Yukon (Lauriol et al. 2006), Puntledge River, British Columbia (Silvestri 2006), Milk River (H.Kling, pers. comm., 2007). Whoriskey (2007) and Lavoie (2006, 2007a, b) cite several affected rivers in the province of Quebec: Bonaventure, Cascapédia, Petite Cascapédia, Nouvelle, Causapscal, Matapédia, Sainte-Anne, and Matane. Unspecified location: Maclement (1917).

CHILE: Lake Sarmiento and Cisnes River (Asprey et al. 1964, Rivera 1983).

CHINA: Khingan, North Manchuria (Skvortsov 1928), Lake Qinghai, Ganzhou (Skvortsov 1935), Chengtu, Szechwan (Skvortsov 1938), Jolmolungma (Jao 1964, Jao et al. 1973, Li et al. 2004), Huogerguos River and Ninxi Forest, Ninshaan County (Stoermer et al. 1986), Changbai Mountains (Bao et al. 1992), Sichuan (Anonymous 1998), Heilongjiang (Yawen et al. 1997, 1998, Li et al. 2004, F.Yawen, pers. comm., 2008), Zhanjiakou (Wen & Zhi-Hui 1999), Xizang Plateau (Huizhong & Jiayou 2000), Hengduan Mountains, Jilin and Xizang (Li et al. 2003, 2004), Lakes Lingza and Gurudongmar, Tibet (CISMHE 2006), Hubei (Wang et al. 2006). Unspecified locations: Ueno (1940), Yawen et al. (1997), Zhixin (2004), Hongjun & Yinxin (2006), Hu & Wei (2006).

CROATIA: Unspecified location (Vouk 1918).

CZECH REPUBLIC: Moravka River (Gágyorová & Marvan 2002, Hašler et al. 2007). Several specimens have also been found in the following rivers: Moravice, Čeladenka, Lučina, Odra, Bečva, Kněhyně, Juhyně, Labe, Borová, Adamovský, and Panský potok (P.Marvan, pers. comm., 2006). Unspecified location: Hindák (1978).

DENMARK: Unspecified location (Mandl 1839).

ESTONIA: Unspecified location (ENSVTA 1970).

FAROE ISLANDS: Agehospital, Skilling (Lyngbye 1819), Unspecified locations: Agardh (1824, 1831), Audouin (1824), Kützing (1833, 1844), De Toni (1891), Cleve (1894), Patrick & Reimer (1975).

FINLAND: Lapland (Wahlenberg 1812, Sommerfelt 1826, Cleve-Euler 1934, Krasske 1943, Kawecka & Olech 2004), Åbo and northern Savo (Cleve 1891), Kuolajärvi (Ramsay & Nyholm 1895), Pojo-Bucht (Mölder 1943, Cleve-Euler 1955), Enontekiö, Henriksnäs, Hötmäinen, Kuusamo, Lojosee, Muonio River, Muostionjoki, Suopohja, Tuohilampi, Vessillanlampi, Viando (Cleve-Euler 1955), Tvarminne (Round 1959), Kilpisjärvi, Tsaikkaljoki (Tynni 1978), Baltic Sea (Hällfors 2004, ICES 2005), Teno River (Komulainen 2005), Tenojoki and Utsjoki Rivers (Miettinen 2006), Nääämöjoki River (Halmeenpää et al. 2007), Northern Ostrobothnia (Niemelä 2007). Unspecified locations: Cleve (1894), Cleve-Euler (1915), Rainio (1973), Eloranta & Kunnas (1979), Kawecka & Eloranta (1987), Tikkanen & Korhola (1993), Soininen & Niemelä (2002), Soininen et al. (2004, 2008).

FRANCE: Chamonix (Brun 1880), Rieu Majou River (Gourdon 1887), Lake Oô (Belloc 1890), Cantal (Héribaud 1893), Gave d'Ossau River (Hustedt 1938), Barjols (Cazaubon 1988), Durance River at Caumont-sur-Durance, and Verdon River at Vinon-sur-Verdon (ASCONIT 2007), Eastern English Channel (Jouenne et al. 2007). Unspecified locations: Bory (1824a), Desmazières (1825), AFAS (1877), Comère (1894).

GEORGIA: Racha (Kukhaleishvili 1985). Unspecified location: Kanchaveli et al. (1981).

GERMANY: Würzburg (Leiblein 1827, Mandl 1839), Erfurt, Thuringia (Kützing 1836), Berlin, Wismar (Mandl 1839), Weserbergland (Suhr 1905, Peter 1913), Isar River, Munich (H.Ullrich & A.Advocat, pers. comm., 2008). Unspecified locations: Oken (1841), Stenzel (1862), Fritsch & Müller (1870), Schenk (1881), Fischer (1903, 1908), Engler & Prantl (1909), Tischler (1934), Harder (1935), Dietrich & Dietrich (1955), Munda (1967), Lange-Bertalot (1996).

GREENLAND: Ivigut (Boyer 1927), Narssaq (Johansson 1980a). Unspecified locations: Jones (1875), Lund (1959).

HUNGARY: Danube River (Backhaus 1968, Literáthy et al. 2002, Ács et al. 2003, 2006, Szabó 2004), Szigetköz (Buczkó et al. 2001-2007, Buczkó 2008, Buczkó & Németh 2008), Lake Mérnökházi (Padisák et al. 2003), Tisza River (Nemes & Matavulj 2004, Szabó et al. 2004, 2005), Maros River (Z.Nagy-László & I.P.Holló, pers. comm., 2004) Several locations in the territory of the Environmental Inspectorate of the North Danubian Region are listed in Érces (2002). Unspecified locations: Maretiae (1924), Donaszy (1959).

ICELAND: Widespread in rivers and lakes (Jónsson et al. 2000, Malmquist et al. 2001, Ólafsson et al. 2004, Jónsson et al. 2006a, b, Magnúsdóttir & Guðjónsson 2006, Jónsson 2007), Lake Thingvallavatn (Jónsson 1987), Háskóla Islands (Magnúsdóttir & Guðjónsson 2006). Unspecified locations: Belloc (1894), Warming & Rosensvinge (1912), Østrup (1920), Hallgrímsson (2007).

INDIA: Kishanganga River (Bhatt et al. 2005, 2008), Teesta River (CISMHE 2006, Bhatt et al. 2007), Ravi, Lachen Chhu and Lachung Chhu Rivers (Bhatt et al. 2008).

IRAN: Jajrood River (Jamallou et al. 2006, 2007).

IRELAND: Londonderry county (Colby & Larcom 1837, Kemp 2006), Carnlough (Hassall 1845), Cork County (Harvey 1845, Hassall 1845), Collin Hill (Schmidt

1899), Caragh (Heuff & Horkan 1984), Killarney (Metzeltin & Lange-Bertalot 1995), Dawros River (Clabby et al. 2004), Galway (Kilroy 2004a), Donegal, Mayo and Sligo (Kelly-Quinn et al. 2005), Burnfoot Ale (Kemp 2006). Unspecified locations: Kützing (1833, 1844), Harvey (1841), Hassall (1845), Fullarton (1846), Rabenhorst (1864), Ward (1864), De Toni (1891), Cleve (1894), Van Heurck (1896), Small (1950), Foged (1977), Chatháin et al. (2004).

ITALY: Courmayeur (Brun 1880), Lakes Como and Bracciano (De Toni & Levi 1886), Laino, Lombardy (Bonardi 1888), Lake Bertignano (Forti 1900), Lake Devero (Monti 1904), Piedmont (Giaj-Levra 1927, M.Battegazzore, pers.comm., 2008), Lake Maggiore (Forni 1925, Giaj-Levra 1927), Lazio (Giaj-Levra & Abate 1994), Trentino (Ciutti et al. 2005, Beltrami et al. 2007, 2008b, c), Natisone, Udine (Zorza et al. 2006), Po and Varaita Rivers (Spaulding 2006, Battegazzore et al. 2007, A. Bertoglio, pers. comm., 2006), Erro River (ARPA Piemonte 2007), Drava River (Beltrami et al. 2008a), Oglio River (E.Arnaud, pers. comm., 2003). Unspecified locations: Mandl (1839), Castracane (1879), Lanzi (1883), De Toni (1891).

JAPAN: Lake Biwa (Negoro 1960). Unspecified locations: Tsumura (1967, 1991), Asai (1995).

KAZAKHSTAN: Lake Bijlikul (Obuchova & Noskov 1966), Ili River (Metzeltin & Lange-Bertalot 1995).

KYRGYZSTAN: Lake Issyk-Kul (Kiselev 1932a, Mambetaliyeva 1963a, b, Kulumbaeva 1982, Metzeltin & Lange-Bertalot 1995), Yassi, Karakuldja, Djaukuchak, Koidjerti and Arabel Rivers, Lakes Sonkul and Chatirkul, Kara-Tyube (Muzafarov 1958).

MALAYSIA: Unspecified location (Shamsudin 1990).

MEXICO: Valle de Bravo (García 2007).

MONGOLIA: Lake Hövsgöl (Dorogostaïsky 1904, Østrup 1908, Ulziikhutag & Tsetsegma 1980, Zagarenko & Prozorov 1980, Kozlov et al. 1989, Kozhova et al. 1994, Edlund et al. 2005, 2006, Genkal et al. 2006), Selenga River (Zagarenko 1983), Tuul River (Soninkhishig et al. 1999), Urd Tamir Gol, Arkhangai (HANNA Database 2007). Unspecified locations: Edlund et al. (2001), Dorofeyuk & Tsetsegmaa (2002).

NETHERLANDS: Unspecified location (ICES 2005).

NEW CALEDONIA: Manguin (1962) [*D. geminata* var. *neocalledonica*: this taxon could not be found in the re-examination of Manguin's original material by Kociolek & de Reviers (1996); the iconotype does not seem to conform with *Didymosphenia* characteristic features].

NEW ZEALAND: Widespread in Southland rivers (Mather 1928, Chapman et al. 1957, Collier & Winterbourn 1990, Kilroy 2004a, b, Campbell 2005, 2008, Duncan et al. 2005, Kilroy 2005, Kilroy & Blair 2005, Kilroy et al. 2005a, b, c, Branson 2006, Duncan 2006a, b, Duncan & Wilkins 2006, Kilroy et al. 2006, Larned et al. 2006, 2007, McNeill et al. 2006, Norton & Sorrell 2006, Thomas 2006, Vieglais & Kilroy 2006, Duncan 2007, Kilroy et al. 2007, 2008). Thomson & Birnie (2005) and Barret (2007) give the following list of affected locations: Buller, Hawea, Clutha, Oreti,

Upper Waiau, Von, Mararoa, Waitaki, Ahuriri, Takaka, Gowan, Pelorus and Speargrass Rivers, and Lakes Manapouri and Dunstan. A complete list of affected waterways is available in Biosecurity New Zealand (2007).

NORWAY: Widespread in Southeastern Norway (Skulberg 1972, 1974, 1982, Lindstrøm 2000), Spitsbergen (Lagerstedt 1873, Cleve 1894, Müller-Haeckel & Solem 1974, Picińska-Fałtynowicz 1988, Metzeltin & Witkowski 1996, Van de Vijver et al. 1999), Tana Elf, Finnmarken (Cleve & Möller 1879), Lake Mjösa (Holmboe 1899 [*G. geminatum* var. *norvegica*], Lindstrøm et al. 1973), Varanger Peninsula (Foged 1968), Glåma River (Skulberg 1972, 1982, Skulberg & Kotai 1978, Skulberg & Lillehammer 1984), Oslo (Brettum 1974), Lake Hammervatnet (Sivertsen 1975), Tanavassdraget (Traqen et al. 1990), Gaula River (Lindstrøm & Rorslett 1991), Barduelva and Troms Rivers (Aagaard et al. 2002), Oyeren (AWI 2003), Svartelva (NIVA 2003), Alta River (Ugedal et al. 2003, 2005, 2006, Koksvic & Reinersten 2008), Hotran Channel (Johansen & Romstad 2006), Gausa (NIVA 2007), Stjørdalselva River (Arnekleiv et al. 2007). Unspecified locations: Agardh (1831), Mandl (1839), Huitfeldt-Kaas (1906), Mölder (1951), Heggberget & Johnsen (1982), Lindstrøm (1991, 1992).

PAKISTAN: Bagah River (Skvortsov 1935), Lake Saiful Muluk (Metzeltin & Lange-Bertalot 1995), Lake Kaghan (Wazir 2002), Dandot (Khattak et al. 2005).

POLAND: Widespread in southern regions (Ligowski & Rakowska 2001, WIOŚ 2002, Mrozińska et al. 2006, Marciniewicz-Mykiet 2007), Litworowego Stawu (Gazdowa 1960), Danube River Basin and Tatra Mountains (Szklarczyk-Gazdowa 1960, Siemińska 1964, Kawecka 1969, 1993, Sanecki et al. 1998, Wołowski et al. 2000, Sanecki 2003), Białka River and Roztoka (Kawecka 1965), Rybi Potok (Kawecka 1965, 1974, 1977), Lake Moskie Oko (Kawecka 1966), Czorsztyn and Sromowce (Mrozińska-Broda & Czerwak-Marcinkowska 1996, 2004), San River (WIOŚ-Jasło 1996, Kawecka & Sanecki 2003), Postolów (Rakowska & Bie'n 2000), Vistula River (Kasza & Galas 2001), Orawska Basin (Noga 2003). Kawecka (1969) and Kawecka & Sanecki (2003) provide the following list of locations: Bialka, Bialy Dunajec, Danube River, Gorce Ranges, Łaczany, Lepietnica Stream, Myczkowce, Niepołomice, Pánszczekki, Pieniny Ranges, Raba River, Roztoka, Rybi Potok, Skawa River, Soła River, Solina, Sucha Woda, and Tarnobrzeg. Unspecified locations: Godlewski (1923), Brockmann (1954).

PORTUGAL: Ave River (Zimmermann 1909).

ROMANIA: Prut River (Şalari 1968), Bicaz water power reservoir (Cărăuș 1973), Bistrita River (Cărăuș 1983a), Lake Izvorul Muntelui (Cărăuș 1983b), Black Sea (Gomoiu & Skolka 1998), Salauta River (Crețu 1999), Tisa River (Hamar 1999), Somesul Cald catchment area (Karina et al. 2000), Somesul Cald River, Doda Pilii (Battes et al. 2000-2001), Florest, Somesul Mic River (Pochon 2002), Rebra, Somesul Mare and Tibles Rivers (Voicinco et al. 2005), Lotru and Sebes Rivers (I.Cărăuș, pers. comm., 2008). Unspecified location: Cărăuș (2002).

RUSSIA: Yekaterinburg (Mandl 1839), Lake Ladoga (Weisse 1865 [*D. geminata* var. *stricta*], Cleve 1891, Schmidt 1899 [*D. geminata* var. *stricta*], Cleve-Euler 1955,

Davidova 1961a, b, 1963, Davidova & Petrova 1968), Okhotsk, Khabarovsk Krai (Grunow 1878, Cleve 1894), Karelian Region (Cleve 1891, Poretzky 1927, 1939, Kiselev 1939, Zabelina 1939, Chernov 1946, 1949a, Lak 1954, 1959, Getsen & Barinova 1965, Komulaynen 1996, 2000a, b, 2001, 2004a, b, 2006a, Genkal & Komulaynen 2000, Komulainen et al. 2005, 2006a, b, Ratkova & Wassmann 2005, Ivanov & Brayzgalo 2007, A.Rusanov., pers. comm., 2006), Lake Onega (Cleve 1891, Wislouch & Kolbe 1927, Metzeltin & Lange-Bertalot 1995), Franz Josef Land and Okhotsk (Cleve 1894 [incl. *G. geminatum* var. *hybrida*], Tsimbalyuk 1955), Ob and Yenisei Rivers (Cleve 1894, Skvortsov 1935, Yakubova 1961, Levadnaya 1965, 1968a, 1986, Skvortsov 1969, Levadnaya & Kuz'mina 1974, Kharitonov 1989a, Shchur et al. 1998, Anufrieva et al. 2003, Gaevsky et al. 2006a, b, Sushchik et al. 2007, Kolmakov et al. 2008), Lakes Kronotskoe, Nerpichje and Nalochevskoe, and Kamtchatka Rivers (Elenkin 1914), Amur River (Skvortsov 1918, Ogly & Kachaeva 1999, Medvedeva & Sirotskiy 2002), Lake Baikal (Junk 1925, Skvortsov & Meyer 1928 [incl. *D. geminata* var. *baicalensis*, *D. geminata* var. *baicalensis* f. *capitata*, *D. geminata* var. *baicalensis* f. *curta*, *D. geminata* var. *baicalensis* f. *curvata*, *D. geminata* var. *baicalensis* f. *elongata*, *D. geminata* var. *curvata* f. *curta*, *D. geminata* var. *curvata* f. *elongata*, *D. geminata* var. *dorogostaiskii*, *D. geminata* var. *dorogostaiskii* f. *curta*, *D. geminata* var. *genuina*, *D. geminata* var. *genuina* f. *baicalensis*, *D. geminata* var. *genuina* f. *curta*, *D. geminata* var. *sibirica* f. *anomala*, *D. geminata* var. *sibirica* f. *elongata*, *D. geminata* var. *sibirica* f. *genuina* and *D. geminata* var. *stricta* f. *baicalensis*], Meyer 1929, 1930 [incl. *D. geminata* var. *genuina*, *D. geminata* var. *baicalensis*, *D. geminata* var. *dorogostaiskii* and *D. geminata* var. *stricta*], Poretzky 1934, Skvortsov 1935, Kiselev 1937a, Skvortsov 1937 [incl. *D. geminata* var. *sibirica* f. *curvata* Skvortsov, *D. geminata* var. *sibirica* f. *subcapitata* and *D. geminata* var. *stricta* f. *curvata*], Kamaruch River (Skvortsov 1927), Lena River (Skvortsov 1935, Kozhov 1953, Skabichevsky 1958, Patrikeeva 1959, Izhboldina 1964, 1970, 1990, Nikolayeva 1964, Cheremisinova 1966, Skabichevsky 1966, 1969, Kofov et al. 1969, Chernyaeva 1970, Dawson 1973a, b [incl. *D. geminata* var. *stricta*], Galazy & Votintsev 1978, Stoermer et al. 1986, Foged 1993 [incl. *D. geminata* var. *baicalensis* f. *curvata* and *D. geminata* var. *sibirica* f. *curvata*], Kiyashko et al. 1998, Kozhova et al. 1998, Kociolek et al. 2000, Popovskaya et al. 2002, Flower et al. 2004, Kravtsova et al. 2004, 2006a, b, Tahteev et al. 2005, Izhboldina 2007, Kravtsova 2007, Pomazkina et al. 2008), Kami River (Shlyapina 1927), Amur-Liman (Kiselev 1931, 1937b), Neva River (Poretzky 1931, Raskina 1968), Laptev Sea (Kiselev 1932b), Tuloma River (Schirschov 1933), Cheshskaya Bay (Virketis & Kiselev 1933), Bolschaya Elduga River (Khakhina 1934), Kola Peninsula (Poretzky et al. 1934, Vodorijin 1936, Cleve-Euler 1955, Komulaynen et al. 1998, Halmeenpää et al. 2007), Stodoly (Chernov 1935), Katun River (Vodorijin 1935, Muzafarov 1958, Yakubova 1961), Kovda (Meyer 1939), Ivan'kov reservoir (Neiswestnova-Shadina 1941, Butorin 1978), Bannaja and Savan Rivers, Kamchatka (Petersen 1946), Konchecero (Chernov 1949b), Neva Bay (Kiseleva 1949), Belaya River (Shtin 1950), Lake Teletskoye (Poretzky & Sheshukova 1953, Anisimova & Belyakova 1997), Lake Frolija (Skabichevsky 1953), Severny Donets River (Proschkina-Lavrenko 1954), Lake Vedlozero (Biske & Lak 1955), Medvejogorks (Sheshukova-Poretskaya 1955), Ojotsk Sea (Juze 1957), Gornyh (Muzafarov 1957),

Sazovo (Muzaferov 1958), Chemal, Kuba and Elikmanar Rivers (Vozjennikova 1958), Taymyr Peninsula (Juze 1959), Kuriles Islands (Kiselev 1959), Lake El'gygytgyn (Juze & Sechkina 1960, Kharitonov 1980, Haritonov 1993a), Kolima (Komarenko 1960), Northwestern Pacific Ocean (Belyaeva 1961a), Sea of Japan (Belyaeva 1961b), Yakimvarskogo Bay (Petrova 1961), Kaliningrad (Sheshukova-Poretskaya 1962), Oskol River (Il'chenko 1963), Angara River (Litninstev 1965, Chernyaeva 1970, Foged 1993, Metzeltin & Lange-Bertalot 1995, Shchur & Lopatin 2005a), Svirj River (Krasnoperova 1967), Jani River (Komarenko 1968), Novosibirsk (Levadnaya 1968b), Primorye Region (Moiseeva 1968, Barinova 1986, Kukharenko 1989, Medvedeva 1999b), Kezhma-Kezhemskom Gulf (Kojova & Zagonenko 1969), Surgutka and Tuba Rivers (Skvortsov 1969), Vitimskom (Endrijinski & Cheremisinova 1970), Pechori River (Getsen 1970), Ingodi River (Kachayeva 1970), Goraisky River (Kukharenko 1972), Kedrovaya and Barabaschevka Rivers (Zhurkina & Kukharenko 1974), Ural River (Poryadina & Ergashev 1975), Volga River (Anonymous 1978), Lake Mayorskoe (Kharitonov 1981), Serebryanka River, Sikhote-Alin reserve (Medvedeva 1981, 1986, 1987, 1994, 1999a, 2000, 2001, 2002a, 2006a, 2008, Barinova & Medvedeva 1996), Prienisey (Arhipov 1984), Berezovyi River (Kukharenko et al. 1984a), Partizanskaja, Malye Melniki and Postyschevka Rivers (Kukharenko et al. 1984b), Anadur River basin (Kharitonov 1986), Sosninsky and Sinuginsky Rivers (Kukharenko et al. 1986), Yamay River (Kuzymin 1986), Krasnoyarskoe Reservoir (Levadnaya 1986), Rudnaja River (Medvedeva et al. 1986), Kolyma Mountains and Yakutia Region (Vasilyeva-Kralina & Gabayshev 1986, Kharitonov 1989a, 2001, Egorova et al. 1991, Potapova 1996, Vasilyeva-Kralina et al. 2005, Haritonov 2006), Iturup Island (Barinova 1989), Anadyr River basin and Magadanskaya Oblast (Kharitonov 1989a), Lake of Jack London (Kharitonov 1989b), Frolovka River (Medvedeva & Nikulina 1989), Lazovka Reservoir (Dogadina & Kukharenko 1990, Gontcharov et al. 2002), Pechenga, Ura and Umba Rivers (Komulaynen 1990), Amgama River (Haritonov 1993b), Kedrovaya Stream (Medvedeva 1995), Ussuri River (Nikulina 1995), Razdolnaya River (Nikulina 1996), Bikin River (Medvedeva 1997, 1999c), Zeva River (Medvedeva 1997, 1999d), St. Petersburg and Murmansk District (Balashova & Zavarzin 1999, Kawecka & Sanecki 2003), Yugorsky-Shar Strait (Lange-Bertalot & Genkal 1999), Burea, Chegdomyn and Urgal Rivers (Medvedeva 1999e), Botchi River (Medvedeva 1999f), Ingoda River and Krasnokamenskoe reservoir (Ogly & Kachaeva 1999), Lake Konchezero (Genkal & Yeshko 2001), Zhelvata River (Kozlovskaya et al. 2002), Kedrovaya Pad Reserve (Medvedeva 2002b), Nefteperarabatyvayuschevo River (Stenina & Zavarzina 2002), Big Cats (Pomazkina & Rodionova 2003), Cheremushnyi Creek (Gol'd et al. 2003), Lake Azabach'e (Lepskaya et al. 2003), Samarga River (Medvedeva & Semenchenko 2003, Medvedeva 2004, Semenchenko et al. 2004), Lake Khanka (Nikulina 2003), Anyui, Aksjanka, Chichimar, Lantar, Khivanda, Rybachja Pad, Tumin, Uda, Uika and Uluikan Rivers (Medvedeva & Barinova 2004), Kuznetsk depression (Tulchinskaya 2004), Vuoksa Lake-River system (Trifonova et al. 2004), Vidlitsa River (Trifonova et al. 2004, Stanislavskaya & Gorchenko 2005), Chelyabinsk Oblast (Yarushina et al. 2004), Kievka River (Medvedeva 2005), Anna River (Nikulina 2005a), South Sakhalin Island (Nikulina 2005b), Razdolnaya River basin (Nikulina 2005c), Krasnoyarsk region (Shchur & Lopatin 2005a, b, Schchur 2006),

Lake Dalneye (Shkurina et al. 2005), Aldan, Anabar, Bilyi, Indigirka, Lena, Olekma and Yana Rivers (Vasilyeva-Kralina et al. 2005), Irtysh River (Bazhenova 2006), Lzhma River (Komulaynen 2006b, c), Barabaschevka and Kedrovaya Rivers (Medvedeva 2006b), Khendergye River (Nazin & Naumenko 2006), Kamtchatka (Shkurina & Belyakova 2006), Podkamennaya Tunguska River (Zadelenov et al. 2006), Novaya Zemlya and Vaygach Island (Genkal & Vehov 2007), Bureya and Tyrma Rivers (Medvedeva 2007, Nikulina 2007, Tiunova 2007), Basseyna River (Nazyn 2007). *Didymosphenia geminata* is currently widespread in East Fennoscandian rivers (Komulaynen 2004c, 2007) and in the Sakha Republic (Komarenko & Vasilyeva 1975, Danilova 2005). Unspecified locations: Georgi (1802), Proschkina-Lavrenko (1950), Zabelina et al. (1951), Getsen (1965), Gollerbach & Krasavina (1971), Skabichevsky (1973), Glezer et al. (1974), Proschkina-Lavrenko et al. (1974), Skabichevsky (1983), Getsen (1985), Barinova & Medvedeva (1988, 2004), Barinova et al. (2000a, b), Komulaynen (2003), Glushchenko & Prokushkin (2005).

SERBIA: Lake Veliko Jačinačko at the north of Sāra Mountain (Urošević 1994), Danube River (Obušković & Maslić 1997), Tisa River (Pujin et al. 1999, Martinović-Vitanović & Kalafatić 2001, Subakov-Simić & Cvijan 2004, Yulić et al. 2008), Sava River (Čado et al. 2006, 2007a), Danube River (Čado et al. 2007b).

SIERRA LEONE: Njala (Carter & Denny 1982).

SLOVAKIA: Vysoké Tatry, High Tatras mountains and Lake Morskie Oko (Bílý 1941), Danube River (Kocinger 2002a, b), Slovak strecth of the Danube River (Hindák & Hindáková 2004), Carpathian mountains (Mrozińska et al. 2006). Unspecified location: Hindák (1978).

SLOVENIA: Moravce (Mašková 2003), Lake Bled (ARSO 2005).

SOUTH KOREA: Unspecified location (Lee et al. 1995).

SPAIN: Huesca (Dosset 1888, Cambra 1989), Aragón (Cleve 1894), Spring Font d'Escorca, Serra de Tramuntana, Mallorca Island (Margalef 1953, Cambra 1991a), Sant Nicolau River, Lake Llebreta, Lake Cavallers, National Park of Aigüestortes, Lérida Province (Margalef 1956, Vilaseca 1978), Ordesa Valley (Cambra 1987, 1991b), Ara River (URS 2006, Blanco & Ector 2008), Revinuesa and Órbigo Rivers (Blanco & Ector, unpub. data). Unspecified location: Álvarez-Cobelas & Estévez-García (1982).

SWEDEN: Lapland (Wahlenberg 1812, Krasske 1943), Västmanland (Agardh 1824, 1831), Östergötland (Agardh 1831), Kjugekull (Cleve 1873, Cleve-Euler 1955), Mälaren (Areschoug 1879, Cleve & Möller 1879, Cleve-Euler 1955), Södermanland (Areschoug 1879, Cleve & Möller 1879), Omberg (Nathorst 1890), Lule Lappmark (Cleve-Euler 1895, 1955), Snavvavagge, Säkokjokk (Hustedt 1924, Cleve-Euler 1955), Lake Vättern (Stålberg 1939, Cleve-Euler 1955, R.Bengtsson, pers. comm., 2007), Abiskojokk, Nissonjokk, Njulja (Hustedt 1942, Cleve-Euler 1955, Skuja 1964), Lake Vänern (Vallin 1951, Wiederholm 1983, Bengtsson 1991, 1992, 1993, 2000, 2001, E.Willén, pers. comm., 2007), Alelyckan, Åreskutan, Lake Åsunden, Ätran River, Deger-berga, Emå River, Göta Älv River, Kerkevare, Kvikkjokk, Lärjeholm, Moortümpel, Njunjes, Lake Öresjö, Lake Siljan, Skövde, Tarrajok, Lake Torneträsk and Värnern (Cleve-Euler 1955), Jämtland (Quennerstedt 1955, Johansson

& Kronborg 1975, Johansson 1979, 1980b, 1982a, b), Lule Alv River (Müller 1962), Tjulån River (Ulfstrand 1967, Carlsson et al. 1977), Kaltisjokk (Müller-Haeckel 1971), Sarekgebirge (AWI 2003), Padjelanta (Wilander 2003), Östersund (Gällerspång 2005), Blekinge, Lakes Åsnen, Helgasjön and Örken Småland, Mörrun and Mörrumsån Rivers, Skåne (R. Bengtsson, pers. comm., 2007). Quennerstedt (1955) reports this diatom in several of the main Swedish rivers. Sonesten et al. (2000) consider *D. geminata* a widespread taxon in southern Sweden, having been found in Värnern, Vättern, Våra rivers, Kållandsö, Åmålsviken and other localities. Unspecified locations: Mandl (1839), Cleve (1894), Foged (1952), Cleve-Euler (1955 [*D. geminata* var. *genuina*]).

SWITZERLAND: Zermatt, Lake Great Saint Bernard (Brun 1880, Hustedt 1930), Lake Geneva (Forel 1904, Hustedt 1930, Druart et al. 1983, Druart & Balvay 2007), Davos (Hustedt 1943), Lake Neuchâtel (Portner 1951), Macun Lakes Region (Robinson & Kawecka 2005), Rivers Aare, Emme (Canton of Berne), Inn (Grisons), Lake Bienna (Hürlimann & Niederhauser 2006), Rivers Rhine, Chur (H.Ullrich & A.Advacat, pers. comm., 2008), Linth, Necker, Thur, Mühlbach, Simmi and Werdenberger Binnenkanal (St. Gallen), Reuss, Altdorfer Giessen, Gangbach and Walenbrunnen (Uri), Rhone near Sierre, Valais (J.Hürlimann, H.R.Preisig & F.Straub, pers. comm.). Unspecified locations: Rabenhorst (1864), Forel (1885), De Toni (1891), Cleve (1894), Meister (1912).

TAJIKISTAN: Amu-Daryi River (Kiselev & Vozzhennikova 1950), Lake Zorkul (Taubayev & Ergashev 1969).

TURKEY: Karasu River (Altuner & Gürbüz 1989, 1990a), Lake Tercan Dam (Altuner & Gürbüz 1990b, Altuner & Gürbüz 1994, 1996), Karasu River (Altuner & Gürbüz 1991), Uzungöl (Şahin 1992, 1998a, Şahin & Gönüloğlu 1999), Çoruh Nehri (Atıcı & Obalı 1997), Şana River (Kolaylı et al. 1997, 1998, Kolaylı & Şahin 1998), Lake Sera (Şahin 1997, 1999), Sera River (Şahin 1998b), Harşit Stream (Bayram & Şahin 2000), Palandöken Pond (Gürbüz 2000), Değirmendere River (Pabuçcu 2000, Kara & Şahin 2001), Lakes Aygır and Balıkçı (Şahin 2000), Lake Dağbaşı (Şahin 2001), Lake Çıldır (Akbulut & Yıldız 2002), Porsuk Pond (Gürbüz et al. 2002), Lake Yedigöl (Şahin 2002), Yanbolu River (Şahin 2003), Lake Çatal (Şahin 2004), Demirdöven Dam (Kıvrak & Gürbüz 2005), Lake Gölköy (Çelekli 2006), Erzurum (Kıvrak et al. 2006), Lake Karagöl (Kolaylı & Şahin 2007). Unspecified locations: Güler & Çobanoğlu (1997), Koray (2001).

UKRAINE: Kharkovskaya, Seversky Donetz (Tonachebskyu & Oksiyuk 1960, Bukhtiyarova 1999b), Maloe Polissya (Vodon'yan 1976, Bukhtiyarova 1999b), Prut River basin (Poluwyk & Garasebuch 1986, Bukhtiyarova 1999b), Tisa River, Rahiv (Bukhtiyarova 1999a, Hamar 1999, Érces 2002). Unspecified locations: Topachevsky & Frantsev (1968), Bazhan (1985), Bukhtiyarova (2000).

UNITED KINGDOM: ENGLAND (including Channel Islands): Guernsey (Salwey 1850), Wray (Smith 1853), Liverpool (Comber 1860), Ambleside (Eulensteine 1867, Bennet 1886), Coquet River, Northumberland (Smith 1874, Brodie & John 2004, Ellwood & Whittton 2007), Strensall Common (Barwell 1882), West Riding (West 1882), Norfolk (Kitton 1884, 1885), English Lake District (West 1892, Pearsall & Pennington 1947),

Devonshire (Schmidt 1899, Harris 1930), Yorkshire (West & West 1901), Tees River (Butcher 1932, Whitton & Dalpra 1968, Holmes & Whitton 1981), Lake Windermere (Goddard 1937), Belle Grange Beck (Douglas 1958), Esthwaite Water (Round 1961), Pentwood Hills (Hoover 1976), Lune River (Holmes & Whitton 1977), Penzance and Omersby (Edgar 1978), Durley Beck and Haweswater (Antoine & Benson-Evans 1984), Pen-y-Ghent (Pentecost 1984), Waterfall Beck (Pentecost 1991a, 2005, Pentecost & Lund 2004), Wealden (Pentecost 1991b), Alwin River (Kelly 2003), Gordale Beck and Barbondale Beck (Pentecost & Lund 2004), Cowside Beck (Gilbert et al. 2005), Ribble Head (Kemp 2006), Pen-y-ghent Gill and Fairmile Beck (A.Pentecost, pers. comm., 2008). Unspecified locations: Berkeley (1833), Greville (1833), Johnston & Tate (1853), Kelly & Whitton (1995a), Sims (1996), Kelly (1998). SCOTLAND: Pentland Hills (Greville 1827, Smith 1853), Lumnsdean-dean River (Carr 1836), Dee and Don Rivers (Dickie 1850), Aberdeen-shire and Ben McDhui (Smith 1853), Gourock (Van Heurck 1884), Tay District (McCall 1933), Shelligan Burn (Egglishaw & Shackley 1971), Isle of Mull (Dawson 1973a), Roberts Linn (Sterrenburg 1973), Moffat Water and Spittal of Shea (Antoine & Benson-Evans 1984), Coquetdale and the Cheviots (Kelly & Whitton 1995b), Gala Water (O'Hare et al. 2005), Ben Lawess (Kemp 2006), Clyde, Annan and Spey Rivers (UKNBN-SEPA 2008), Ardle River (M.A.Tiffany, pers. comm., 2008). WALES: Cader Idris (Hassall 1845), Dolgellau (Hassall 1845, Ralfs 1850, Smith 1853), Black Mountain District (Erichsen Jones 1949), Wye River (Antoine & Benson-Evans 1983, 1984, 1985, 1986a, b), Afon Aran (Antoine & Benson-Evans 1984), Ely River (Antoine et al. 1984, Esho & Benson-Evans 1984). Unspecified locations: Turton (1807), Agardh (1831), Kützing (1833, 1844), Mandl (1839), Goldsmith (1840), Harvey (1841), Ralfs (1843), Hassall (1845), Queckett (1850), Carpenter (1856), Notcutt (1859), Anonymous (1862), Rabenhorst (1864), Knight (1867), Ward (1869), Lang (1873), Morehouse (1876), Anonymous (1884), De Toni (1891), Cleve (1894), Van Heurck (1896), Merlin (1910), Heron-Allen & Earland (1911), Taylor (1929), Zahar (1951), Fryer (1963), Lucas (1969), Macan (1970), Garnett (1973), Whitton (1975), Edgar (1978), Metzeltin & Lange-Bertalot (1995), AWI (2003).

UNITED STATES: Mackinaw Island (Bailey 1842), Niagara River (Kützing 1849, De Toni 1891), West Roxbury (Stodder 1859), Newcastle county (Tatnall 1860), Lake Michigan (Briggs 1872, Thomas & Chase 1887, Marsh 1895, Ward 1896, Chase 1902, Britton 1944), Buffalo (Day 1882), Connecticut (Terry 1907), Taunton River (Sedgwick et al. 1912), Philadelphia (Boyer 1916), Massachusetts (Weston & Turner 1917, Webber 1961), Delaware River and Chicago (Boyer 1927), Indiana (Palmer 1930, Lindsey et al. 1969), Cayuga Lake Basin (Burkholder 1931), New York State (Hohn 1951), Lake Superior (Fox et al. 1967, 1969, 1973, Nelson et al. 1973, Stoermer 1980, 1993, Stoermer et al. 1986, Moffat 1994, HANNA Database 2007, M.Edlund, pers. comm., 2007), Virginia State College farm pond (Woodson 1969), Provo River (Lawson & Rushforth 1975), Virginia (Patrick & Reimer 1975), Great Lakes (Stoermer 1975, Stoermer & Kreis 1978, Stoermer et al. 1999, Quinlan et al. 2007), Colorado (Aronson 1976, M.Edlund, pers. comm., 2007), Wyoming (USGS 1978), Colorado River (LeRoy Poff et al. 1990, Niyogi et al. 2002, Opsahl et al. 2003, Brown 2008), Montana (Bahls 1993, Sensibaugh 2002), Stanislaus River (Wilcox et al. 1994), Idaho (Pryfogle et al. 1997), West Saint Louis Creek (Rader &

Belish 1997), Chesapeake Bay (ICPRB 1998, Lacouture 2001, Marshall et al. 2005, Blankenship 2008), Alamo River (Lange & Tiffany 2002), Lake Beaver (Rhodes 2003), Rapid Creek, Black Hills (Erickson et al. 2004, Anonymous 2006, Erickson & Shearer 2006, Shearer & Erickson 2006, Simpson 2006, USDA Forest Service 2006, Backlund 2007, Larson 2007, Ranney et al. 2007), Kootenai River (Holderman & Hardy 2004, Glass 2005, Marshall 2008), White River, Arkansas (Anonymous 2005a, Shelby 2006a, b), Toboggan Creek (Remington & Lough 2005), Tennessee River (Schroeder 2005), Boulder Creek (Spaulding 2005, Murphy 2006), South Fork American River (Tarbell 2005), Blackfoot River (Weber 2005), Castle Creek (MICRA 2006), Lake Roseboud (PPL Montana 2006), Rocky Mountain National Park (Wanty et al. 2006), Middle Popo Agie River (WGFD 2006), Vermont (Allen 2007, Wacker 2007, A.Shambaugh pers. comm., 2007), Yellowstone (Anonymous 2007a), Glacier National Park (Bahls 2007b), Fish Creek (HANNA Database 2007), New England (Anonymous 2007b, Rathke 2007, Daley 2008), Watauga, South Holston, Norris Dams, Smith and Jackson Rivers (Rohde 2007), Cache la Poudre River (Sterrenburg et al. 2007, M.Edlund, pers. comm., 2007), Connecticut River (Waterbury 2007), Elk River (Preston 2008), Baltimore (Michael 2008, Pfeiffer 2008a, b), Middle Fork Flathead River (Wyatt et al. 2008), Mad River (Waterbury 2008), New Hampshire (A.Shambaugh, pers. comm., 2007). ALASKA: Lake Karluk (Judy et al. 1932, Stoermer et al. 1986), Utukak and Colville Rivers (Patrick & Freese 1961), Sagavanirktoq, Umiat, Brooks Range and Anchorage (Foged 1981), Cook Inlet (Sheath et al. 1986), Hancock and Henderson counties (Grubaugh et al. 1988), Tanana River (LaPerriere et al. 1989), Adak Island (Hein 1990), Kuparuk River (Miller et al. 1992), Barrow, Lake Tangle and Salmon Creek (Nagumo 1993), Toolik (Sheath et al. 1996, M.Edlund, pers. comm., 2007), Ivishak River (Parker 1999), Chester Creek (Zheng 2002), Blueberry Creek (Edwardson et al. 2003), Kijik River (Brabets & Ourso 2006a), Crescent River (Brabets & Ourso 2006b), Anchorage (ANSP 2007), Coopers Landing and Denali National Park (M.Edlund, pers. comm., 2007). UNSPECIFIED LOCATIONS: Queen (1862), Wolle (1890), Palmer & Keeley (1900), Grainger (1952), Palmer (1959), Peabody & Burgess (1984), Dufford et al. (1987), Sheath & Cole (1992), Stevenson (1997), Reimer et al. (2001), Bahls (2004), Benke & Cushing (2005), Cardinale et al. (2006), Hambrook et al. (2007), Kumar et al. (2009). Elwell (2006) gathers ~200 confirmed records of mass-growth of *D. geminata* in the states of Alaska, Arizona, Arkansas, California, Colorado, Idaho, Missouri, Montana, Nevada, North Carolina, North Dakota, South Carolina, South Dakota, Tennessee, Texas, Utah, Virginia, Washington, West Virginia. Further locations are listed in Stoddard et al. (2005).

UZBEKISTAN: Samarkanda (Kiseleva 1939), Isfaramsai (Muzaferov 1958), Boz-Su and Jazarbaj Canals (Ergashev 1968). Unspecified location: Ergashev & Alimzhanova (1989).

Discussion

1. Distribution

The performed bibliometric study indicates that, despite references to *D. geminata* in the phycological literature have increased exponentially since early XIX century,

the relative frequency of publications concerning this species has not increased accordingly. This reflects the existing poor knowledge regarding the biology of *D. geminata*. This situation may start to reverse from the acknowledgement of its negative environmental impact.

The distribution of fossil or subfossil records of *D. geminata* (Fig. 1) may provide the primitive biogeographical area covered by this taxon. This seems to be a relatively recent species (Mackay et al. 2002) more closely related to cymbelloid-like diatoms than to gomphonemoid-like ones (Kociolek & Stoermer 1988, Moffat 1994, Papas 2008). The earliest record is a Pliocene diatom assemblage from the Fusong area, China (Jiaying & Yuzao 1986). According to Okuno (1964), this species is a Pleistocene relict (>11000 BP), being dated for the Pleistocene period in certain deposits on Long Island, USA (Lohman 1939). The first accurately dated records in Europe corresponded to the early Weichselian (~11000 BP) in Finland (Sarmaja-Korjonen & Alhonen 1999, Eriksson et al. 1999, Miettinen et al. 2002), and the late Devensian in Scotland, Loch Sionascaig (Pennington et al. 1972, Haworth 1976). The distribution of fossil records of *D. geminata* is apparently restricted to the Holarctic region, and corresponds essentially to its native geographical range, which covers the whole of the Northern Hemisphere above the 30°N parallel (Fig. 5). Currently, the Sierra Leone record (Carter & Denny 1982) is the southernmost one, but this observation in West Africa has to be checked. Kociolek & Spaulding (2000) state that such restricted distribution exemplifies the overall patterns of regional endemism in diatoms; however, the data presented in this study support the idea of a much broader global distribution.

Metzeltin & Lange-Bertalot (1995) and Kilroy et al. (2005b) summarized the current knowledge on the distribution of *D. geminata*, but our results point out that several references have been neglected to date, especially older studies, and those related to southern Eurasia. According to Elwell (2006), the first record of this diatom in North America corresponds to Cleve (1894), however several earlier reports exist, e.g. Bailey (1842), Kützing (1849), Briggs (1872), Day (1882), Thomas & Chase (1887). This species was not reported or not detected in the Southern Hemisphere until it was first discovered in New Zealand by Mather (1928), although massive *D. geminata* growths have been occurring only since 1990s. An older, very doubtful citation from 1880 exists also for Australia in Victoria (Day et al. 1995, Entwistle & Nairn 2007). In South America, only few citations with illustrations of *D. geminata* exist for Chile in Lake Sarmiento and Cisnes River (Asprey et al. 1964, Rivera 1983). In New Zealand, strong environmental policies have prevented *D. geminata* expansion to surrounding areas, and it now seems to be confined to Southland, where it is continuously expanding its geographic distribution. Nevertheless, a global distribution map based on ecological niche models (McNyset & Julius 2006) shows suitable ecosystems for this diatom in several regions of the Southern Hemisphere. South American rivers in Argentina, Chile and Peru (Spaulding & Elwell 2007, Kumar 2008) are especially vulnerable to *D. geminata* invasion and this is very likely to happen if biosecurity protocols are not implemented. In Europe, its distribution has been historically circumscribed to high latitudes (e.g. Brun 1880, Krammer & Lange-Bertalot 1986), but its presence has also been detected as a sporadic species in some inventories from the Mediterranean region, both in fossil and recent

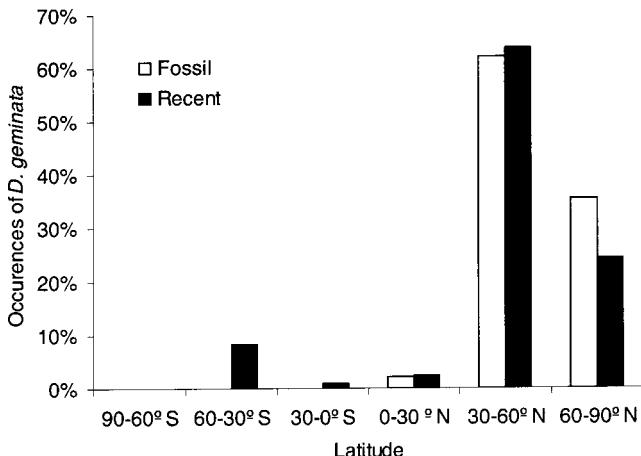


Fig. 5: Occurrence (%) of *Didymosphenia geminata* in the different geographic latitudes.

records (Blanco & Ector 2008). Presently, it forms nuisance benthic growths with a large spatial coverage, and temporal persistence in South Poland (Kawecka & Sanecki 2003), and North Italy (Beltrami et al. 2008a, c), as well as massive mucilaginous mats, that have recently been detected in the Spanish Pyrenees (Ara River, Ebro River basin, URS 2006) and the Duero River basin (Blanco & Ector, unpub. data).

Reports of mass developments of *D. geminata* date back to the 19th century: northern and western rivers of the United Kingdom have been exposed to large masses of *D. geminata* for over 150 years (Elwell 2006). Greville (1827) found massive growths of this diatom in Scotland, filamentous mats were present in Ireland in 1836 (Fullarton 1846), high biomasses were reported from Norwegian streams (Skulberg & Lillehammer 1984), and massive growths were reported in China in 1935 (Skvortsov 1935). West (1904, 1916) mentions greyish felt-like masses of *D. geminata* attached to the rocks of mountain streams and cataracts. Also, clogging effects have been first described in 1951 in Sweden (Vallin 1951). Hence, excessive growths do not only appear in areas where this species is presumably exotic.

On the other hand, rapid expansion is not a worldwide biogeographic pattern for *D. geminata*. For instance, this species was once generally distributed in the Great Lakes (North America) but now it is restricted to Lake Superior (Stoermer 1993). In some Iceland streams the distribution and coverage of *D. geminata* decreased between 1996 and 1997 (Jónsson et al. 2000). Likewise, *D. geminata* seems to have disappeared from Japanese freshwaters where, apart from two unspecified locations (Tsumura 1991, Asai 1995), only fossil records have been found.

2. Ecology

Kilroy et al. (2005b, 2007) provides a comprehensive summary of the ecology of *D. geminata*. Like many gomphonemoid species, it inhabits periphytic communities,

thanks to its ability to produce attachment stalks. In fact, the negative impact of *D. geminata* is related, to a large extent, to the production of high amounts of extracellular polymers organized in stalks. The ability to secrete large quantities of highly organized extracellular polymer arrays differentiates this from other related benthic diatoms (Gretz et al. 2006a, b, 2007a, b). Specimens with stalks of several centimetres in length are typical. Mats of stalk material, which usually include trapped sediments, accumulate and cause unsightly masses. These growths create a microenvironment that can be colonized by diatoms and other organisms (Kilroy et al. 2005a, Kelly 2006). It is believed that this growth strategy allows *D. geminata* to compete with other algae for both nutrients and light (Hoagland et al. 1993). Despite being a predominantly benthic organism, *D. geminata* was also found in planktonic samples of the Danube River in Slovakia (Obušković & Maslić 1997, Hindák & Hindáková 2004); *D. geminata* may even become the dominant taxon in the phytoplankton and phytobenthos in Himalayan Kishanganga River (Bhatt et al. 2005).

Older diatom literature regards *D. geminata* as a good indicator of cold oligotrophic and xenosaprobic waters of low conductivity (e.g. Rabenhorst 1853, Rawson 1956, Sládeček 1973, Patrick & Reimer 1975, Wolf 1982, Krammer & Lange-Bertalot 1986). In the United States, this taxon indicates low nutrient concentrations (Potapova & Charles 2007). However, there is increasing evidence that the autecological profile of this species has changed in recent decades. According to Kawecka & Sanecki (2003), *D. geminata* has a wider ecological range than has been assumed to date. Its recent expansion in Eastern Europe, especially in Poland, points to a wider tolerance of nutrient conditions. The discovery of nuisance *D. geminata* populations in high nutrient waters was the first recognition that the species was appearing outside its acknowledged ecological range (Gunde-Cimerman et al. 2005, Kilroy et al. 2005a, Sterrenburg et al. 2007). In Poland and the United States, mass developments are appearing in eutrophic rivers (Kawecka & Sanecki 2003, Elwell 2006, Spaulding & Elwell 2007), and Miller et al. (1992) found a fast and positive response of this species to phosphorus fertilization. This change seems to affect also its temperature tolerance: growth of *D. geminata* is favoured by high temperatures (~20°C) in Wales (Wye River, Antoine & Benson-Evans 1986a), Canada (Vancouver Island streams, Rieberger 1991), and in Turkey (Değirmendere River, Kara & Şahin 2001), but the opposite trend has been observed in Southern Poland flowing waters by Noga (2003). Growth peaks of this species in Turkish rivers occur in spring between April and June (Kolaylı et al. 1998, Kara & Şahin 2001, Şahin 2003) whereas growth of *D. geminata* tends to be most prolific in summer in British (Kelly 2006) as well as in Canadian streams (Mundie & Crabtree 1997). Kilroy et al. (2005b) conclude that, although this diatom appears to be confined to cold areas, it reaches its highest biomass at higher water temperatures within these localities.

Didymosphenia geminata exhibits a strong dependence on hydrodynamic conditions (Sutherland et al. 2007) and substrate stability, being considered indicative of high water discharge conditions (Blinn & Herbst 2003). In fossil deposits its presence testifies to the flow-through regime of the water body (Olyunina 2005). However, in New Zealand this alga grows in a very broad range of river conditions, and it is not very selective regarding water depth or speed of the river flow (Anonymous

2005b). According to Kilroy et al. (2005b), low flows in summer and higher flows in winter appear to favour its growth, suggesting that flow conditions over the previous winter determine whether massive *D. geminata* growths will occur or not in the following winter. Several studies (Skulberg 1982, Kawecka & Sanecki 2003, Kelly 2006, Kirkwood et al. 2007, Spaulding 2007) state that *D. geminata* seems to be proliferating in streams subjected to flow regulation worldwide. Moreover, it can withstand much stronger floods than other algal species (Anonymous 2005b). High flows may detach the thicker mats, contributing to the dispersion of this alga (Hansen 2003, Holderman & Hardy 2004). Additionally, several studies confirm that *D. geminata* requires stable substrates in order to establish a population (Cox 1996, Kravtsova et al. 2004, Kilroy et al. 2005a, Kelly 2006). Sutherland et al. (2007) detected poor survival of *D. geminata* in spring-fed creeks; however, no single environmental variable could be identified as being responsible for this effect.

The ecological preferences of *D. geminata* regarding other abiotic factors are not well known. With reference to dissolved minerals, the European Water Framework Directive protocols consider this taxon as a reference species for calcareous running waters (Schaumburg et al. 2005), though it may also grow in rivers receiving drainage from both peaty soils and limestone (Kawecka & Sanecki 2003). Finally, Lindstrøm & Rorslett (1991) consider *D. geminata* as a highly metal-sensitive species; however, Oberholster et al. (2005) found this species as the dominant diatom in long-term coal tar-contaminated sediments.

3. Nuisance effects

Mass growths of *D. geminata* have a large spatial extent. Stalks formed by this diatom may cover almost all available benthic substrates, forming dense mucilaginous, gelatinous mats up to several centimetres thick, and up to 20 km in length (Spaulding et al. 2005a, Elwell 2006, Lagerstedt 2007). Mass developments can also form along the margins of lakes (Kilroy et al. 2005a). Mats may reach nearly 100% in coverage of the stream substrate in some locations (Shearer & Erickson 2006), and consist predominantly of polysaccharides (Stevenson et al. 1996). Periphyton containing a high percentage of polysaccharides may not be as palatable or nutritious as other forms of algae that have higher lipid and/or protein content (Holderman & Hardy 2004). Furthermore, dense mats prevent the growth of other macroalgae, which are an important source of food for aquatic invertebrates (Spaulding et al. 2005a). Hence there exists a correlation between the presence of large populations of *D. geminata*, the decrease in abundance of some aquatic invertebrate species, and the increase in chironomids (Brown 2008). This leads to a general decrease in species richness within zoobenthos (Mundie & Crabtree 1997). In New Zealand areas where this diatom has become established, macroinvertebrate populations have increased; however, they tend to be smaller species, with greater proportions of taxa that are generally associated with polluted waters, and considered poor quality food for fish (Anonymous 2005b). In streams severely affected by *D. geminata*, invertebrate populations decrease, macrophytes are eliminated, and fish are virtually absent (Jónsson et al. 2000). In the United States and Iceland, a decline in fishery industry has been concurrent with the expansion of *D. geminata* (Jónsson et al. 2000, Shearer

& Erickson 2006, Cook et al. 2008). Freshwater fish populations may also be negatively affected due to the lack of suitable conditions for spawning areas (Shelby 2006a, Boubée et al. 2008), and due to significant diurnal dissolved oxygen fluctuations associated with *D. geminata* mats (Kilroy et al. 2005a, Stohlgren et al. 2007).

Another generally reported negative impact is the clogging and fouling of water intakes, causing problems in hydro-power canals (Josselyn & Fiorillo 1993, Pryfogle et al. 1997, Willén 2001, Kilroy et al. 2005a, Anonymous 2005b, Packman et al. 2008) and even hampering the use of river water in supply systems (Kawecka & Sanecki 2003).

The causes that have led to such dramatic changes in the ecology and growth patterns of *D. geminata* are poorly understood. Sherbot & Bothwell (1993) suggested that high levels of ultraviolet radiation may promote growth; however, this hypothesis has been criticized by Elwell (2006). On Vancouver Island, waters of impacted catchments have lower buffering capacity than unaffected rivers (Sherbot & Bothwell 1993). In Lake Baikal the expansion of *D. geminata* has been related to the detrimental effect of industrial waste waters (Kozhova et al. 1998) and Ellwood & Whitton (2007) state that organic phosphate as a major P source is a key factor favouring the success of *Didymosphenia*. However, in Iceland the distribution and biomass of extensive mats appeared to be unrelated to water chemistry (Jónsson et al. 2000). According to some authors (Kilroy et al. 2005a, Ács et al. 2006), increasing occurrence of invasive *D. geminata* may be attributed to a genetic variant that has broader tolerances than the original species. Within diatoms, strong environmental changes can promote the evolution of locally adapted lines that eventually speciate (Shayler & Siver 2004). The presence of mass developments, dated from early 19th century in Europe, may point to an environmental or anthropogenic cause rather than a genetic process beneath this ecological change.

Current experimental control strategies for *D. geminata* that have been proposed (see Gee & Wells 2006 for a review) include treatments with Organic Interceptor®, certain enzymes (Jellyman et al. 2006), chelated copper (Jellyman et al. 2006, Clearwater et al. 2007, Wells et al. 2007), and sodium chloride (Matheson et al. 2007), although the efficacy of these methods has not been thoroughly determined. Experimental results (Lee et al. 2008) show that *D. geminata* blooms are resilient to scour. Kilroy (2005) and Kilroy et al. (2006) review the results of several decontaminating treatments both in situ and in laboratory experiments.

As in the case of *D. geminata*, the introduction of exotic diatom species has been confirmed in several occasions (e.g. Harper 1994, Kühn 1997), and the dispersion mechanisms of these microalgae are discussed in Coste & Ector (2000). According to Bhattacharya et al. (2008) for Indian Himalayan rivers, the introduction of exotic fish species (e.g. brown trout) might be also responsible for the dispersal of *D. geminata*. There is a general agreement that the introduction of *D. geminata* outside its native distribution area is caused by human vectors (Elwell 2006, Vanormelingen et al. 2008), therefore further worldwide spread of this species is probably inevitable (Kilroy et al. 2005a). Molecular techniques for the early detection of *D. geminata* cells are being currently developed (Cary & Hicks 2006, Cary et al. 2007b, Hicks et al. 2007).

National and international management strategies should promote public awareness programmes, along with strong environmental policies devoted to preventing the spread of this nuisance invasive organism. Further research is encouraged in order to assess the ecology and the dispersion patterns of this diatom, its influence on flora and fauna in rivers and lakes, and potential economic impact assessment.

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