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Research Article

The arrival and spread of the bloom-forming, freshwater diatom, *Didymosphenia geminata*, in New Zealand

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Abstract

Blooms of the stalked diatom *Didymosphenia geminata* (Lyngbye) M. Schmidt, 1899 have been increasingly reported worldwide since the 1990s. In 2004, the appearance of blooms in New Zealand, for the first time, highlighted the invasive nature of this organism. In the absence of previous reliable records for this species, *D. geminata* was assumed to be non-indigenous and a nationally coordinated biosecurity response was initiated in an attempt to contain it. We examined the spread of *D. geminata* over five years using presence/absence data from national and regional delimiting surveys, combined with information from local agencies on potential vectors and data from national recreational angling surveys. Use of a rigorous sampling method raised confidence in the accuracy of negative results. Survey results supported the 2004 assumption that *D. geminata* was a recent arrival. Incremental but rapid spread to many South Island rivers from two main foci (the Mararoa and Buller Rivers) suggested mass dispersal of an invasive organism via human vectors. The distribution of affected rivers relative to angler usage data for 2007-08 was consistent with angler-mediated dispersal from catchment to catchment. This conclusion was supported by local information about likely vectors of *D. geminata* to individual sites. Other potential vectors were considered important (e.g., kayaking and power boats) but no river usage datasets were available to verify the patterns. At the time of writing *D. geminata* had not been detected in the North Island. Although *D. geminata* has been detected in a high proportion of South Island rivers, blooms have a more restricted distribution. The extent, drivers and impacts of these blooms are the subject of ongoing studies.

Key words: non-indigenous species, human-mediated dispersal; sampling, rivers, delimiting surveys

Introduction

Invasive microorganisms are common in the marine environment (e.g., Drake et al. 2007), but free-living microscopic algae have rarely been reported as invaders in freshwaters. One of the few examples of a potentially invasive freshwater micro-alga is the stalked benthic diatom *Didymosphenia geminata* (Lyngbye) M. Schmidt, 1899 (Figure 1A), which can form unusually high biomass in rivers by producing prolific quantities of stalk material (Kilroy et al. 2009) (Figure 1B,C). In the Northern Hemisphere *D. geminata* has attracted the attention of river managers and ecologists following reports of unprecedented blooms since about 1990 (e.g., Jonsson et al. 2000; Kawecka and Sanecki 2003; Bothwell et al. 2009). Such mass developments were recognised as unusual, but the events were not described as invasions because *D. geminata* was either known to be already present in the affected regions, or there was no information from which to determine previous presence or absence.

In 2004, perceptions about this species shifted when unusual algal blooms in the Southland region of the South Island, New Zealand, were identified as *D. geminata*. In the absence of any reliable previous records in New Zealand, *D. geminata* was assumed to be a non-indigenous species. Because of its bloom-forming capabilities, within a few weeks of its discovery *D. geminata* was declared an "unwanted organism" by Biosecurity New Zealand (MAF-BNZ), part of the New Zealand Ministry of Agriculture and Forestry and the Government agency responsible for biosecurity. Subsequently, *D. geminata* blooms have been shown to have measurable effects on benthic communities in New Zealand rivers (in particular benthic invertebrate community composition and abundance), as well as reported aesthetic and economic effects (Kilroy et al. 2009) (Figure 1B, C).

Similar effects of *D. geminata* blooms on benthic invertebrates have been reported in other locations (e.g. Canada; Gillis and Chalifour 2009). A striking feature of *D. geminata* is its tendency to form the highest biomass in low-nutrient rivers (Whitton et al. 2009; Bothwell and Kilroy 2011, but see also Kawecka and Sanecki 2003) not normally susceptible to algal blooms, which are typically induced by high nutrients (Biggs 2000). Since 2004, *D. geminata* blooms have continued to expand their global range in both Europe and North America (e.g., see Blanco and Ector 2009), and most recently South America (Segura 2011).

Following the first reports of *D. geminata* blooms in New Zealand in 2004, review publications on the genus have cited older records and implied that *D. geminata* may have been present in New Zealand much longer (Whitton et al. 2009; Blanco and Ector 2009). In that case, the recent appearance of blooms in Southland may be a phenomenon similar to that reported on Vancouver Island, Canada, where *D. geminata* was known to have been present historically (first record in 1894), but the occurrence of blooms was new (Bothwell et al. 2009). For both Vancouver Island and New Zealand, anglers were primarily implicated as the most likely vector, especially via the use of felt-soled wading boots (Bothwell et al. 2009).

In this paper we explore the progression and drivers of the *D. geminata* invasion in New Zealand. We first summarise the evidence for the historical presence or absence of *D. geminata* in New Zealand. We then describe the spread of *D. geminata* during the five years since the appearance of the first blooms in Southland in 2004. We used survey data, local knowledge, and published data about river usage to address two questions: (1) is the pattern of spread of *D. geminata* within the South Island consistent with spread of a newly arrived species via human activities, and (2) what were the likely relative roles of angling versus other activities and non-human vectors?

Didymosphenia geminata in New Zealand: support for historical absence

A literature and data search for previous records of *D. geminata* (and earlier synonyms including *Echinella geminata* Lyngbye and *Gomphonema geminatum* (Lyngbye) Agardh) in New Zealand was conducted at the time of the first 2004 appearance of *D. geminata* blooms. Literature

Figure 1. Microscopic and macroscopic *Didymosphenia geminata*. **A**. Light micrograph of live cells with stalks. Cells are approximately 120 μm long. **B**. *D. geminata* bloom in a braid of the dam-regulated Waitaki River, South Island, New Zealand, November 2009; **C**. A *D. geminata* mat, against a background of a didymo bloom exposed by falling river level in the Waitaki River, March 2007 (Photo credits: **A**, **B**, Cathy Kilroy; **C**, Shirley Hayward).

examined included formally published checklists of algae and diatoms, as well as recent algal taxa lists from regional surveys, especially in Southland. Since the initial evaluation of the non-indigenous status of *D. geminata*, we have re-examined pre-2004 data and samples from the catchment in which the first blooms were discovered, and from the South Island in general.

The only comprehensive checklist of diatom species in New Zealand (Cassie 1984) was based on earlier checklists of algae and other literature. A single record of *Gomphonema geminatum* (from Melling Ditch, Hutt Valley, North Island [exact location now uncertain; assumed to be in or near the suburb of Melling], Mather 1928) was cited. We found no further published or unpublished records of *D. geminata* (or its synonyms) from either the North or South Islands.

Mather's study, as described in the original copy of her thesis (Mather 1928), included collecting monthly algae samples from 18 sites in the Hutt Valley between November 1926 to September 1927, along with habitat information. Samples were analysed for taxonomic composition, but neither the methods, nor microscope type, nor magnifications used for examining and identifying specimens were described.

G. geminatum was listed as "common" in a sample collected from Melling Ditch in August 1927, but was not listed in any of the other ten monthly samples for this site. *G. geminatum* was mentioned at one other nearby site (Stokes Valley Stream) by Mather (1928), but the name was struck out on the manuscript, and no score assigned. The species list for that site continued with *Gomphonema constrictum*, implying that Mather (1928) had initially identified the specimens as *G. geminatum*, but then rejected the identification in favour of *G. constrictum*. The two taxa are somewhat similar in shape, although *G. constrictum* is smaller. *G. constrictum* was recorded at seven of the 18 sites (including at Melling Ditch).

The two-page bibliography in Mather (1928) did not list any specialised texts on diatoms except for studies from New Zealand, but a general text on freshwater algae (West 1904) included an illustration of *G. geminatum* and *G. constrictum* side by side. However, Mather (1928) did not illustrate of any of the algae listed in the thesis. The only mention of illustrations (apart from photographs of some of the sampling sites) is a single reference to drawings of species

where the identification was doubtful. There is no indication that the thesis ever included those drawings, or that voucher specimens of the collections were kept.

In the absence of illustrations, voucher specimens, and discussion of the growth form of diatom species in the text, it is impossible to verify or reject the identification of *G. geminatum* in samples from Melling Ditch. However, all our observations on the habitat requirements of *D. geminata* indicate that a shaded, near-stagnant, sand–silt-lined ditch liable to dry out, as recorded by Mather (1928), is an unlikely habitat for this species (e.g., Kilroy et al. 2008; Kumar et al. 2009). Furthermore, Mather's inclusion of *Gomphonema constrictum* as well as *G. geminatum* in the species list from Melling Ditch, and her apparent indecision over the species' identity at Stokes Valley Stream, raises the plausible scenario that she misidentified larger specimens of *G. constrictum* as *G. geminatum*. Published size ranges for the two species indicate overlap in cell length, but not in cell width (*D. geminata*, length 60–140 μm; width 25–43 μm; *Gomphonema truncatum* Ehrenberg 1832 (syn. *G. constrictum* Ehrenberg 1832), length 13–75 μm; width 7–17 μm, Krammer and Lange-Bertalot 1997). *G. constrictum* has been recorded at sites throughout New Zealand (Cassie 1984), although recent sample collections indicate that the species is rarely abundant (CK, personal observations).

New Zealand's freshwater diatom flora has been well studied, with at least 49 publications focusing on diatom species published from 1853 to 1980 (Cassie 1983). Many of these publications were based on collections for eminent European diatomists who would have been familiar with *D. geminata*. For example, the diatom collection of J.D. Raeside includes extensive cleaned diatom material from rivers throughout the South Island, mostly dating from the 1960s, and has recently been catalogued and cross-referenced. Despite a comprehensive literature collection (including European monographs that contain drawings of *D. geminata*), *D. geminata* (or its synonyms) is not on any of the lists of hundreds of taxa Raeside identified from New Zealand, and there are no drawings of it (M. Bothwell and N. Raeside, pers. comm.).

Between the mid-1980s and 2004 there was considerable research on river periphyton in New Zealand, mainly focusing on management of nuisance growths (e.g., Biggs and Price 1987;

Biggs and Smith 2002). Most of these studies included taxonomic analyses of samples. In particular, periphyton samples from almost all major South Island rivers now affected by *D. geminata*, and numerous other rivers in both North and South Islands, were examined in the "100 Rivers Study" (Biggs 1990; Biggs et al. 1990), with no records of *D. geminata* (B. Biggs, pers. comm.). While *D. geminata* has been frequently recorded in fossil and subfossil diatom samples in other parts of the world (Blanco and Ector 2009; Pite et al. 2009), the species has so far not been reported in such samples in New Zealand (see references in Cassie 1983), or in more recent lake deposits (e.g., Reid 2005; Mildenhall et al. 2006).

Since 1996, annual periphyton monitoring has been carried out in late summer in the Lower Waiau River, where *D. geminata* blooms were first discovered. Up until 2004, over 250 samples had been examined microscopically at magnifications of 100× to 400×. No specimens of *D. geminata* were found until 2005. We have re-examined samples collected by Environment Southland in the Mararoa River in February 2004, at the site of the assumed first incursion (refer to Results) and at sites downstream. We detected no specimens of *D. geminata*. Although there are records of *D. geminata* and *G. geminatum* in the Allan Herbarium (CHR), Landcare Research, Lincoln, New Zealand they are specimens from material collected from overseas (V. Cassie, pers. comm.).

Materials and methods

Surveys for Didymosphenia geminata since 2004: procedures

The status of *Didymosphenia geminata* as an "unwanted organism" in New Zealand prompted MAF-BNZ to initiate a nationally coordinated response (Vieglais 2008), with eight nationwide surveys to document its spread conducted between October 2005 and November 2007 (http://www.biosecurity.govt.nz/pests/didymo/where-is-it). Survey sites were selected to include rivers thought to be most susceptible to invasion, while ensuring complete geographical coverage (Duncan and Wilkinson 2006). Sites on individual rivers were chosen assuming human-mediated spread, and on the basis of estimated ecological suitability (Kilroy et al. 2008). Sites were generally removed from the survey once

D. geminata had been detected, but some were resampled if no visible colonies appeared. Since 2008, surveys have been conducted by local agencies. Standard sampling procedures (see below) were used in all surveys.

To maximise the chances of detecting *D. geminata* cells if they were present in a river, a field protocol was developed based on sampling recently invaded river systems at a range of distances downstream from areas with visible *D. geminata* growth (Kilroy and Dale 2006). The trials showed that a 10-minute deployment of a 40 μm-mesh, 200 mm-diameter opening plankton net, facing upstream in the river thalweg yielded samples that were always positive for *D. geminata* at sites up to 60 km downstream from visible colonies. Material collected in the net was concentrated into a 120 ml container. Cells were usually detected in benthic samples at downstream sites, but at the cost of greater sample analysis effort. Benthic samples comprised the combined algae scraped from 20 rocks collected along four transects or partial transects up to 10 m apart, extending out to depths of up to 0.7 m. To minimise the chances of false positives at subsequent sampling sites, a strict protocol of cleaning and disinfecting all equipment was adhered to following each sample collection (Duncan et al. 2007).

In the laboratory, at least three 1–2 ml subsamples from each net and benthic sample were scanned (standard total time of 15 minutes per sample) under an inverted microscope at 100×. The presence of live or recently alive *D. geminata* cells (i.e., containing chloroplasts) signified a positive result. Where only empty frustules were found the sample was deemed "suspect positive", and the site was re-sampled at the earliest opportunity. During the surveys, additional sampling often followed positive finds in new rivers, to establish the upstream limit particularly if the find was reported as visible colonies.

For surveys in the North Island, use of a rapid-throughput, highly sensitive genomic detection method (Cary et al. 2008) has enabled high-frequency surveillance over a wide area, as well as high confidence in negative prediction. Plankton net samples only are required for this analysis, using a modified net design (Hicks et al. 2007).

Data

MAF-BNZ maintains an internet-based database intended to provide a single-source registry of the results (both positive and negative) of all surveys for *Didymosphenia geminata* throughout New Zealand (https://www.didymosamplesdb.org.nz/). In addition to samples collected and analysed using the techniques described above, the database includes positive records when *D. geminata* was detected at the stage of visible growth. For the present study, we downloaded the database, comprising 3357 records up to 23 December 2009, representing 229 positive sites (Appendix 1) and 1126 negative sites. These records covered all territorial authority regions in New Zealand except the northernmost region (Northland). For each site, we derived its segment in the New Zealand River Environment Classification (REC), a spatial network of linked segments covering all New Zealand lake and river systems (Snelder and Biggs 2002). Linkage to the REC allowed each site to be mapped in relation to upstream and downstream river segments in the same catchment. The REC also specifies stream order (a measure of upstream catchment complexity) for every river segment, which ranges from 1 for the smallest headwater streams to 8 for the largest mainstem rivers.

We used the locations of both positive and negative sites on the MAF-BNZ database to map the spread of *D. geminata* in New Zealand annually from 2004 to 2009. Positive sites were mapped as river lines on the assumption that, once present at a site upstream, downstream spread was inevitable. Negative sites were mapped as points, because there was no way of knowing whether *D. geminata* was not already present downstream.

We classified all 229 positive records into one of the following three pathway categories, where the term "pathway" described different types of movement (*sensu* Wilson et al. 2009):

1. new: a positive site in a new catchment or sub-catchment with no previous positive records;

2. downstream: a positive site in a catchment which already has positive sites upstream;

3. upstream: a positive site in a catchment which already has positive sites downstream.

Potential vectors

D. geminata cells may remain potentially viable for at least 50 days in damp, cool (e.g., 12°C or less) conditions (Kilroy et al. 2007). Therefore,

transfer from one site to another was believed to be feasible via many different means.

To identify potential vectors of *D. geminata* for each positive site, we contacted local agency staff familiar with rivers and river sites in their region. Agencies included the Department of Conservation (DOC), Regional Councils, and Fish and Game New Zealand (FGNZ). For each site in their region identified in the database as positive for *D. geminata*, we asked about site usage, significance for recreation, as well as the specific question: in your expert opinion, what was (were) the most likely vector(s) of *D. geminata* into that site? We requested consideration of all possible vectors, both human and non-human (e.g., birds, wild animals). As far as possible we obtained information from at least two organisations for each site.

In addition, we examined the relationship between *D. geminata* distribution and recreational angling using data from FGNZ surveys. In New Zealand, recreational angling for acclimatised freshwater fish is managed by FGNZ with an annual fishing licence system. FGNZ licences are interchangeable among regions except for the Lake Taupo region, North Island, which is managed separately by DoC and was therefore not included in the present analysis. FGNZ has used national surveys of its licence holders to estimate annual effort for all recognised river and lake fisheries every 6–7 years since 1994/95 (Unwin 2009), including data on the proportion of the effort on each river associated with visitors from other FGNZ regions. The most recent (2007/08) survey included overseas visitors to New Zealand as a separate stratum, allowing their fishing patterns to be contrasted with those of New Zealand residents (Unwin 2009).

For the present study we limited our analysis to rivers fished for at least 500 angler-days during the 2007/08 angling season (1 October 2007 to 30 September 2008), where an angler-day is defined as one angler fishing on one day without regard to the number of hours fished. These fisheries (236 in total) accounted for 93.7% of the total estimated river fishing effort for the 2007/08 season. In addition to total angler usage for each fishery (94.6% of which was recorded by New Zealand residents), we derived three metrics of angler origin based on each respondent's home address and FGNZ region. These were: 1) the proportion of the total annual usage contributed by New Zealand visitors from outside the local region; 2) the total
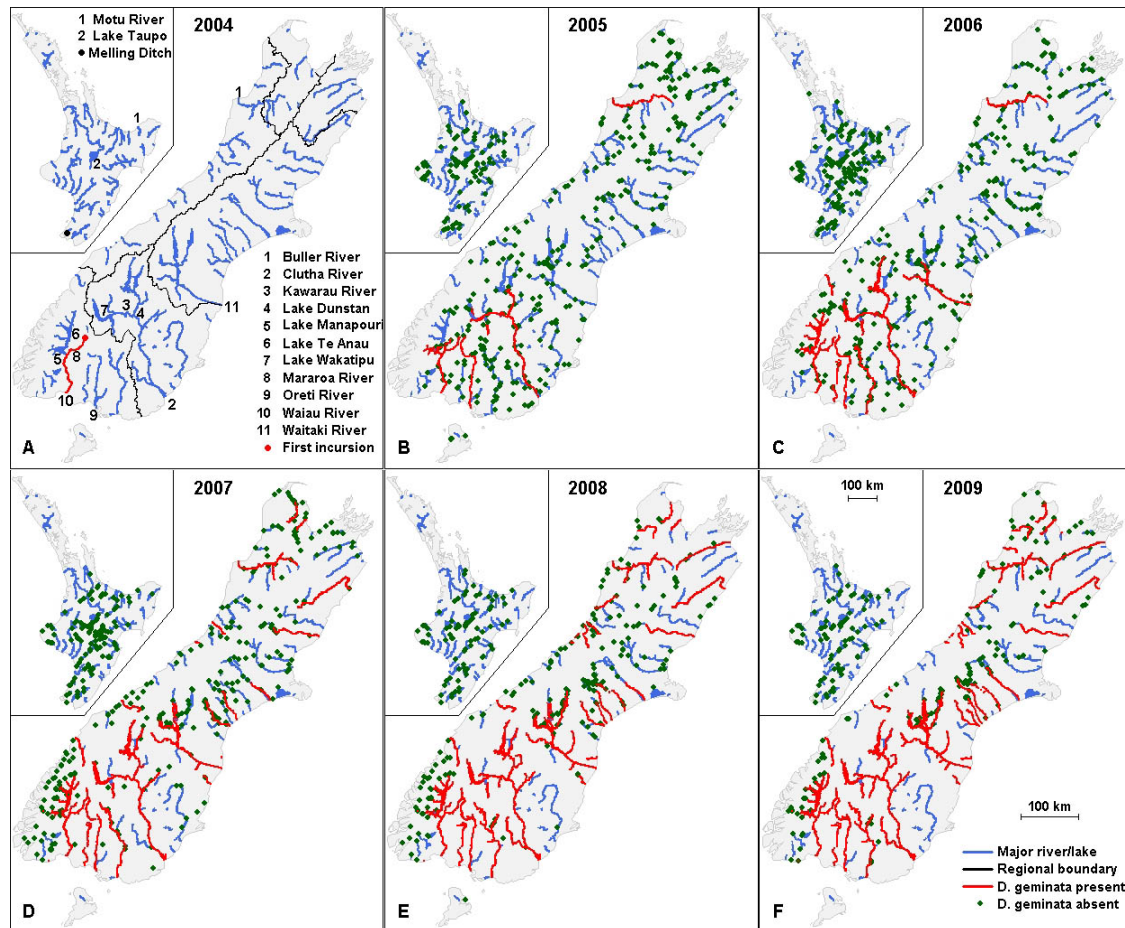
Figure 2. Spread of *Didymosphenia geminata* in the South Island of New Zealand, 2004-2009. Locations referred to in the text are indexed in panel A, together with the location of the first reported incursion on 20 October 2004. The North Island (inset) is shown at half scale.

annual usage (angler-days) by overseas visitors; and 3) the proportion of the total annual usage contributed by overseas visitors. The distribution of each metric was compared with the distribution of positive *D. geminata* sites at 23 December 2009.

Results

The spread of Didymosphenia geminata in the South Island, 2004 – 2009

Didymosphenia geminata blooms were first discovered in the lower Waiau River on 20 October 2004. The assumed first point of incursion was 70 km upstream in a tributary of

the lower Waiau, the Mararoa River. This was determined by tracing the bloom upstream to a footbridge with public access to the river, above which no *D. geminata* was observed until approximately 9 months later (author's observations). After its discovery in the Mararoa and Lower Waiau Rivers, *D. geminata* was not detected in any other catchment until September 2005, when visible growth was reported almost simultaneously in four other rivers (Figure 2B). These were the upper Waiau River, which is physically separated from the lower Waiau River by Lake Manapouri; the Oreti River, the upper catchment of which is contiguous with the Waiau catchment; and the Clutha River and Buller River, at sites approximately 100 and 450 km,

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Table 1. Numbers of sites in South Island rivers testing positive for *Didymosphenia geminata* by year and pathway category (new, downstream, upstream), 2004–2009.

Year	new	downstream	upstream	Total
2004	1	1		2
2005	11	5	1	17
2006	6	9	13	28
2007	33	15	41	89
2008	7	10	23	40
2009	5	7	41	53
Total	63	47	119	229

respectively, from the initial incursion site. *D. geminata* was not detected in any other catchment in 2005. The annual reporting rate for new positive sites increased from 2005 to 2007 (Table 1). Upstream dispersal has been the dominant source of new positives since 2007. Spread from the Buller River followed a similar pattern to that from the lower Waiau River, in that 15 months elapsed between first discovery in the upper Buller River (24 September 2005) and the first positive in another catchment in that area (Figure 2). By the end of 2007 the diatom was established over most of the South Island, followed by slower range expansion in 2008 and 2009.

Discovery and reporting of new positive sites was strongly related to stream order, particularly during the first two to three years after the first incursion. By early 2006, the entire lengths of New Zealand's two order 8 rivers (the Clutha and Waitaki) were positive. By the end of 2009, over 81% of the length of all South Island order 7 river segments and over 56% of order 6, were positive (Table 2). This tendency is an inevitable consequence of way in which stream order is defined within a river network, which ensures that it increases monotonically with increasing distance downstream, but does not necessarily imply that lower order streams are less susceptible to *D. geminata*. Relatively few streams of order 3 or lower have been surveyed, but the presence of the diatom in some first order streams confirms that – given time – it has the potential to spread upstream well into the headwaters of catchments in which it is present. At the time of writing, *D. geminata* has still not been detected in many east-coast catchments of the South Island, or in any North Island waterways.

Vectors

From the interviews, we identified twelve distinct vectors which could have contributed to the spread of *Didymosphenia geminata* in South Island rivers (Table 3). Excluding natural downstream dispersal, all but two (livestock and wildlife) were directly associated with human activity. Of the 229 positive sites, 139 were considered to be associated with one vector, 71 with two, and 19 with three.

Anglers were considered to be the most likely vector associated with new incursions (28 of 47 sites), with kayaking implicated in one third of new incursions (13 of 47 sites). Assessments were based on observations of first occurrences of *D. geminata* just downstream of well-known angling locations or kayak put-in sites. Seven other vectors were considered potential vectors for new incursions at 19 out of 47 sites (40%), of which the most prevalent were power boats; hydroelectric or irrigation canals; and 4WD all-terrain vehicles. General recreation based on family activities such as picnicking and swimming were potential vectors for new incursions on two rivers, while field staff responsible for tasks such as river gauging, and gold mining, were each potentially linked to one new incursion. Animal vectors (domestic livestock and wildlife) were not considered likely vectors for any new incursions.

A more diverse range of vectors were thought to be responsible for upstream incursions (Table 3). Angling (72 of 119 sites) was the most commonly implicated, but at least one of eight other human mediated vectors was a potential vector at over two thirds (69%) of the sites in this category. In addition, animals (domestic livestock and non-domestic wildlife) were potential vectors at 28 sites on 26 rivers. Most of these were small streams in areas where the land use was dominated by pastoral farming, and involved small tributary streams no more than 5 km upstream from a primary source. In particular, upstream incursions in numerous small streams in rural areas were potentially mediated by domestic livestock.

Obvious associations with human-induced vectors were only rarely associated with downstream dispersal of *D. geminata*. Power boats were considered potential vectors in 15 of 63 such cases, most of which were shoreline or river mouth sites in Lake Te Anau (10 sites), or shoreline sites in Lake Dunstan (4 sites). The Kawarau River was the only river where power

Table 2. Chronology of *Didymosphenia geminata* incursions in South Island rivers by year and stream order (Strahler system, where the smallest headwater streams are first order), based on downstream traces using NIWA's River Environment Classification (REC) scheme. Successive columns for each stream order show the total length of river segments mapped in the REC downstream of a sement identified as positive for *D. geminata*.

Stream order	Total length (km)	2004	2005	2006	2007	2008	2009	Total, all years	% of total length
1	132 605		5	4	7	23	8	48	0.0%
2	56 992			1	19	7	5	32	0.1%
3	28 841		1	9	22	1	11	44	0.2%
4	14 602		19	8	147	79	112	365	2.5%
5	6 801	47	97	136	323	307	194	1 105	16.2%
6	3 455	14	203	373	643	579	125	1 938	56.1%
7	947	96	259	161	125	83	45	769	81.2%
8	337		196	141				337	100.0%
Total	244 579	157	778	834	1 286	1 078	501	4 634	1.9%

Table 3. Vectors implicated in the spread of *Didymosphenia geminata* in South Island rivers versus pathway category (new, downstream, upstream), 2004–2009. Figures shown in each cell are the number of sites for which the corresponding vector was implicated, as a count and (in parentheses) as a percentage of the total sites in that category.

Vector	Pathway			
	new	downstream	upstream	Total
anglers	28 (60%)	4 (6%)	72 (61%)	104 (45%)
power boats	5 (11%)	15 (24%)	15 (13%)	35 (15%)
kayaks	13 (28%)	3 (5%)	17 (14%)	33 (14%)
livestock			23 (19%)	23 (10%)
vehicles	4 (9%)		17 (14%)	21 (9%)
general recreation	2 (4%)	4 (6%)	14 (12%)	20 (9%)
trampers			12 (10%)	12 (5%)
diversion canal	5 (11%)	1 (2%)	3 (3%)	9 (4%)
wildlife			10 (8%)	10 (4%)
field staff	1 (2%)		3 (3%)	4 (2%)
gold mining	1 (2%)		2 (2%)	3 (1%)
downstream dispersal		63 (100%)		63 (28%)
Number of sites	47	63	119	229

boats were considered likely to have been responsible, following previous incursions in three Lake Wakatipu tributaries.

Angling usage analysis

The presence or absence of *Didymosphenia geminata* in relation to angler usage estimates and categories of angler origin suggested a relationship between angler activity and the current distribution of the organism in the South Island. Rivers where *D. geminata* was present tended to be more heavily fished than those where it was absent (Figure 3). Median annual angler usage for rivers where *D. geminata* was present was 1730 days, compared to 911 days for rivers where it was absent.

Data on fishing activity by angler origin, as indexed by the region within which their fishing

licence was purchased (see Figure 2A) also suggested an association between angler mobility and the presence of *D. geminata* (Figure 4A). In the South Island the diatom was rarely found in rivers for which local anglers (i.e., anglers fishing within the region in which they purchased their licence) accounted for 90% of more of total usage, irrespective of their level of usage. Rivers where *D. geminata* was present tended to receive at least 10% of their usage either from anglers visiting from other New Zealand regions, or from overseas visitors. The areas having the highest proportions of overseas angling activity include the headwaters of the Waiau, Mararoa, and Oreti Rivers in Southland, the Buller River and its tributaries, which encompass the two sites (Mararoa River and Buller River) which now appear to be the source of all subsequent incursions (Figure 2).

Figure 3. Presence or absence of *Didymosphenia geminata* in 107 South Island rivers with an estimated 2007/08 angling usage of at least 500 angler-days. Vertical arrows denote median angler usage for each histogram.
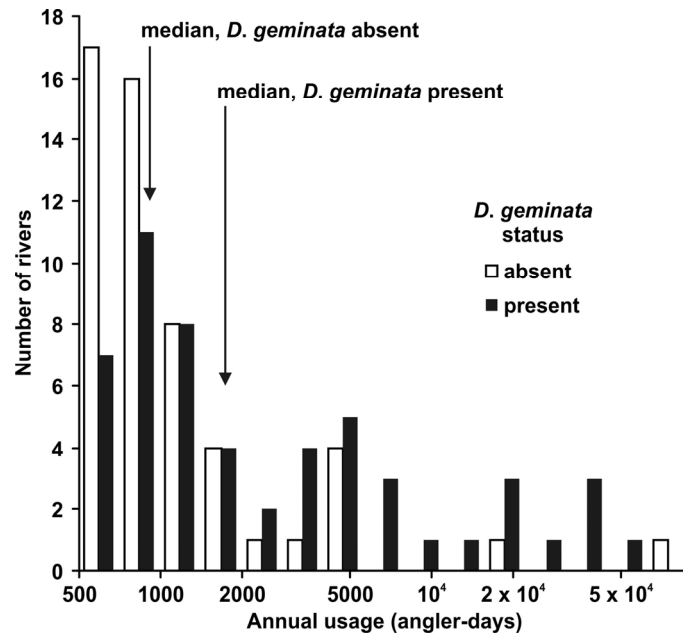
Angler mobility patterns for North Island rivers tend to be more muted than for their South Island counterparts. Few rivers derive more than 10% of their total annual effort from overseas visitors, and movement of anglers between New Zealand regions is also comparatively restricted (Figure 4b). Overseas visitors accounted for more than 50% of total 2007/08 usage for only one North Island river in the dataset (the Motu).

However, this estimate is subject to considerable uncertainty because of the relatively low usage for this river (510 ± 240 (1 SE) angler-days, only just above the 500 angler-day threshold for this analysis), and the correspondingly high coefficients of variation associated with the estimated overseas and New Zealand contributions to this total (300 ± 220 and 210 ± 110 angler-days, respectively).

Discussion

The failure to record *Didymosphenia geminata* in numerous algae and diatom surveys of South Island rivers before the Mararoa River discovery, its rapid dispersal to other South Island rivers over the next 3–4 years by predominantly human vectors, and the highly equivocal nature of the single historical record of the species in New Zealand, strongly suggest that the 2004 event represents a new incursion of a non-indigenous invasive species. We find no evidence to support the suggestion that *D. geminata* was present in New Zealand for many years previously (Whitton et al. 2009; Blanco and Ector 2009).

If *D. geminata* had been present in the Mararoa/Waiau catchment before 2004, we believe it would almost certainly have been detected during either the 100 Rivers Study (Biggs et al. 1990; Biggs 1990), or in the detailed annual periphyton monitoring surveys of these rivers which began in 1996. The extensive surveys to document the spread of *D. geminata* in New Zealand since 2005 further support the conclusion that the species is non-indigenous. Numerous sites recorded as negative for *D. geminata* in the earlier surveys subsequently became positive. In all cases of new incursions into a catchment, there was an obvious human vector. There have been repeated demonstrations in New Zealand that if *D. geminata* is present upstream in a river, then plankton net sample collection methodology (as used in the *D. geminata* surveys) will detect it (authors' unpublished data). The net method has also shown that *D. geminata* may be present in a river even when visible growths have never been
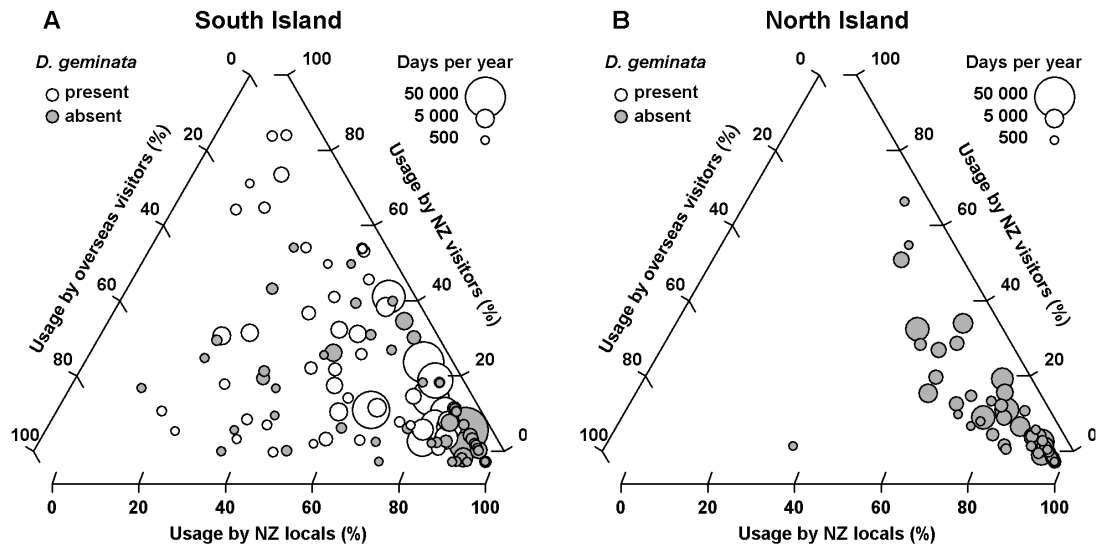
Figure 4. Presence or absence of *Didymosphenia geminata* in rivers with an estimated 2007/08 angling usage of at least 500 angler-days, vs. angler origin, for 107 South Island rivers (A) and 51 North Island rivers (B). The radius of each plotting symbol is scaled as the cube root of total annual usage.

reported. Therefore we have confidence that negative surveys reflected absence of *D. geminata* upstream. Furthermore, continued failure (at the time of writing) to detect *D. geminata* in North Island rivers, despite use of a highly sensitive genomic technique (Cary et al. 2008), reinforces our view that *D. geminata* was never indigenous there.

A similar conclusion regarding nonindigenous status was reached for the nuisance alga *Hydrodictyon reticulatum*, which was first recorded the North Island, New Zealand, in 1986 (Coffey and Miller 1988), again on the basis of the absence of previous records of a very distinctive species. Nevertheless, considering the challenges demonstrating absence of a microscopic organism from a region, *D. geminata* could reasonably have been classed as a cryptogenic species (*sensu* Carlton 1996) at the time of the 2004 discovery. The status of other potential invaders have been similarly uncertain. For example, the gastropod *Batillaria australis* is currently distributed across both eastern and western Australia. However, it has recently been shown to be most likely non-native

in Western Australia, and to have significantly affected estuarine ecosytems in that region (Thomsen et al. 2010).

A potential caveat to our conclusions is the long-standing paradigm of ubiquitious dispersal of free living micro-organisms (Finlay 2002, Finlay et al. 2002), which implies that micro-organisms can never be responsible for invasions. However, recent tests of the paradigm with respect to freshwater diatoms have concluded that although many diatom species certainly have very broad distributions, dispersal limitation appears to play a significant part in determining the characteristic taxonomic composition of regions (e.g., Vyverman et al. 2007). Therefore it should be no surprise that *D. geminata* was not present in New Zealand long before the 2004 discovery of blooms. At least one other diatom genus (*Hannaea*) appears to be absent from the New Zealand freshwater diatom flora, as well as many species. The prolonged viability of *D. geminata* cells in cool, damp conditions (Kilroy et al. 2007) suggests ease of dispersal of live cells into New Zealand, for example by air in personal items (Tatem

2009). On the other hand, maintenance of suitable conditions for survival during natural long-distance dispersal via wind or animal vectors seems unlikely (Kociolek and Spaulding 2000)

Regardless of the prior presence or absence of *D. geminata* in New Zealand, the pattern of spread of the organism in the South Island indicates an invasive organism. Indeed, recent definitions of invasions do not always require non-indigenous status (or even detrimental impacts) (e.g., Valéry et al. 2008). This would imply that proliferations of *D. geminata* on Vancouver Island and in mainland USA (Kumar et al. 2009), for example, could have been viewed legitimately as invasions. To our knowledge, the possibility that the bloom-forming *D. geminata* differs genetically from the endemic species in those locations has yet to be resolved.

Human-mediated spread between catchments

Reports from representatives of local agencies on rivers affected by *Didymosphenia geminata* yielded consistent confirmation of a plausible human-mediated vector in all cases of new incursions to catchments. The broad pattern of spread is also consistent with a human-mediated process. Wilson et al. (2009) described six types of dispersal pathway for invasive species (mainly non-indigenous terrestrial plants), referring to the type of physical movement in terms of frequency of movement, distance moved, and number of propagules involved in each event. Although humans may facilitate any of the pathways, human-mediated dispersal is particularly characterised by "mass dispersal", as well as the deliberate transfer of species through cultivation. Mass dispersal is described as "a dispersal route …. such that many individuals can move from different parts of the range to many new sites". This is considered to be a type of long-distance dispersal. In other words, the new sites are too far distant from the source site for natural dispersal to have been responsible in most cases (with exceptions for migratory birds, for example). The spread of *D. geminata* throughout the South Island since 2004 is consistent with mass dispersal because of its almost simultaneous appearance in multiple, widely separated rivers, over a short time span (e.g., compare 2005 and 2007 in Figure 2). The rapid pace of spread also suggests human involvement.

Types of potentially natural dispersal proposed by Wilson et al. (2009) are leading edge dispersal; corridor dispersal; jump dispersal; and extreme long distance dispersal. Leading edge dispersal is defined as "gradual changes in range initiated by individuals colonising new areas from the edge of the range (diffusive spread)". This is what we see when *D. geminata* spreads downstream in a river (via flow), and upstream (via unknown natural vectors, which might include fish, invertebrates, and birds). Corridor dispersal is diffusive spread to suitable habitat via a recently formed physical connection such as a land bridge (natural) or canal (man-made). Analogies for *D. geminata* include spread through inter-catchment diversion conduits, e.g., irrigation canals. Jump dispersal implies long-distance dispersal but with some intermediate connection, and could include possible transfer of damp *D. geminata* cells within or between catchments by birds. Extreme long-distance dispersal for *D. geminata* is analogous to the rare, human-mediated event(s) in which viable propagules were initially transported to New Zealand.

The patterns shown are consistent with different vectors operating at different spatial scales (e.g., Pyšek et al. 2008). In the case of *D. geminata*, our data suggest human-mediated dispersal between continents and catchments, and natural dispersal within catchments (both upstream and downstream).

In common with descriptions of the spread of some other invasive species (e.g., Johnson and Padilla 1994; Aldridge et al. 2004; Karatayev et al. 2009), our conclusions regarding vectors rely on circumstantial evidence. No data exist to prove that a certain vector type (human or otherwise) has been responsible for introducing *D. geminata* to a particular site. However, the responses regarding potential vectors for *D. geminata* at each affected site strongly implicated anglers as the most likely vector for most new and upstream incursions and the angler usage data were consistent with this. Our results are consistent with the circumstantial evidence presented by Bothwell et al. (2009), who linked the use of specialised felt-soled waders favoured by anglers to the spread of *D. geminata* into at least 14 rivers on Vancouver Island between 1988 and 1994. Data on usage by anglers of rivers in New Zealand are assembled only every 6–7 years (compared to annually for some rivers on Vancouver Island), so were not able to gauge whether the spread of *D. geminata* between

rivers and regions may have been influenced by inter-annual variability in angler usage. Therefore in identifying different patterns of angler usage on *D. geminata*-affected and non-affected rivers, we have not allowed for inconsistent angling pressure from year to year. Another difficulty in interpreting the data arises because the association found with anglers could also reflect that rivers which are ecologically susceptible to *D. geminata* are also attractive for angling. Nevertheless, the *combination* of the local responses regarding likely vectors and the pattern of affected rivers versus angler usage is compelling evidence for a real connection. Furthermore, the data also show that in the South Island, rivers free of *D. geminata* tended to be those with highest levels of usage by local anglers (Figure 4). This is consistent with the tendency for angling in New Zealand to be predominantly a local activity, with a median travel distance (home address to the nearest point on each river fished) of 43 km, and 77% of anglers fishing within 100 km of home (NIWA, unpublished report available on request). The pattern of mainly local angler usage in the North Island (albeit excluding the major Taupo fishery) suggests that if *D. geminata* were present there and assuming favourable river environments, then we would expect large scale dispersal via anglers to be slower than that seen in the South Island.

Although the circumstantial evidence implicating angler-mediated spread seems reasonably clear, our conclusions should not be interpreted as implying that angling is the most important vector. Our ability to demonstrate a link between angler activity and new *D. geminata* incursions reflects the scope and quality of FGNZ's angler survey data as much as the role of anglers in facilitating its dispersal. However, the striking correspondence between the sites where *D. geminata* was first detected in the south and north of the South Island, and the regions in which overseas anglers account for the highest proportion of total angling effort, supports the assumption that the arrival of *D. geminata* in New Zealand was via angling equipment. Indeed, we cannot rule out the possibility that the original incursions in the Mararoa and Buller Rivers were independent events, particularly given the relatively slow spread of the diatom into rivers draining to the South Island west coast.

Lack of data for other river-based recreational activities, such as jet-boating or kayaking, means that their involvement in the spread of *D. geminata* remains speculative. Nevertheless, the circumstantial evidence is compelling. For example, the available information on kayaking / rafting rivers certainly suggests an association with *D. geminata* presence in some regions. Several West Coast rivers in which *D. geminata* has been recorded are far from population centres of any size, but are likely to be visited by groups of kayakers travelling the length of the Coast in search of paddling opportunities.

The spread of *D. geminata* around the South Island, New Zealand, has occurred in spite of a nationwide campaign to encourage river users to decontaminate all equipment, clothing and vehicles, before use in another river (http://www.biosecurity.govt.nz/pests/didymo/cleaning). However, the campaign may have helped ensure the continued failure to detect *D. geminata* in the North Island, as may a ban in 2008 on the use of felt-soled waders (http://www.fishandgame.org.nz/Site/Features/Features_Media020908.aspx). Local measures also appear to have slowed the spread into highly valued areas such as southern Fiordland (http://www.doc.govt.nz/upload/documents/parks-and-recreation/plan-and-prepare/didymo-control-fnp.pdf).

Didymosphenia geminata presence and blooms

The presence/absence data available for tracking the spread of *Didymosphenia geminata* in New Zealand are insufficient to document the impact of *D. geminata*. The survey data examined show that *D. geminata* is present in a high proportion of high order river reaches in the South Island. However, field observations indicate that in many cases presence does not lead to blooms. In some rivers repeatedly found to be positive in net samples, visible growth is rarely or never observed and benthic samples are often negative (authors' unpublished data). Furthermore, after 6 years of spread around the South Island it is clear that some rivers are resistant to *D. geminata*, with several large catchments still apparently free of the species. Therefore, the high level of infestation indicated in Figure 2F does not imply a similar level of impact. Whether resistance to *D. geminata* colonisation extends to North Island rivers, or whether absence there represents successful uptake of spread-prevention measures is currently unknown. Environmental factors affecting *D. geminata* distribution and the extent, drivers, and impacts of blooms are the subjects of ongoing studies.

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Supplementary material

The following supplementary material is available for this article.

Appendix 1. Records of *Didymosphenia geminata* in the South Island, New Zealand, 2004–2009, showing the date of first detection for each site.

This material is available as part of online article from:
http://www.aquaticinvasions.net/2011/AI_2011_6_3_Kilroy_Unwin_Supplement.pdf