Original article

Didymosphenia geminata invasion in South America: Ecosystem impacts and potential biogeochemical state change in Patagonian rivers

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ABSTRACT

The diatom Didymosphenia geminata has emerged as a major global concern, as both an aggressive invader of rivers and streams in the southern hemisphere, and for its ability to form nuisance blooms in oligotrophic systems in its native range. South American D. geminata blooms were first documented in Chilean Patagonia in May 2010, and have spread to over five regions and three provinces, in Chile and Argentina respectively. The Patagonian invasion represents a distinct challenge compared to other regions; not only are affected systems poorly characterized, but also a general synthesis of the nature and magnitude of ecosystem impacts is still lacking. The latter is essential in evaluating impacts to ecosystem services, forms the basis for a management response that is proportional to the potentially valid threats, or aids in the determination of whether action is warranted or feasible. Based on a revision of the recent literature, some of the most significant impacts may be mediated through physical changes: substantially increased algal biomass, trapping of fine sediment, altered hydrodynamics, and consequent effects on biogeochemical states and processes such as redox condition, pH and nutrient cycling in the benthic zone. Surveys conducted during the early invasion in Chile show a strong correlation between benthic biomass and associated fine sediments, both of which were one–two orders of magnitude higher within D. geminata blooms. Experimental phosphorous amendments showed significant abiotic uptake, while interstitial water in D. geminata mats had nearly 10–20 fold higher soluble reactive phosphorous and a pronounced pH cycle compared to the water column. A dominant and aggressive stalk-forming diatom with this combination of characteristics is in sharp contrast to the colonial cyanobacteria and bare gravel substrate that characterize many Patagonian streams. The potential displacement of native benthic algal communities with contrasting functional groups, increased primary producer biomass, and fine benthic sediment accumulation, all may have a significant effect on stream nutrient cycling and ecosystem function, in Patagonia and elsewhere where nuisance blooms have been reported.

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1. Introduction

Didymosphenia geminata has attracted considerable attention as a nuisance species within its native range (Spaulding and Elwell, 2007; Blanco and Ector, 2009; Whitton et al., 2009) and as an aggressive invader and in the southern hemisphere (Kilroy and Unwin, 2011; Reid et al., 2012). A substantial body of published and gray literature has accumulated in recent years, documenting *D. geminata* distribution and range expansion (Blanco and Ector, 2009; Whitton et al., 2009; Kilroy and Unwin, 2011), modeling potential habitat (Spaulding and Elwell, 2007; Kilroy et al., 2008;

Kumar et al., 2008), risk and impact assessment (Beville et al., 2012; Cliff and Campbell, 2012) and evaluation of biological impacts (Floder and Kilroy, 2009; Kilroy et al., 2009; Miller et al., 2009). Only a few studies have focused on ecosystem impacts, albeit indirectly via mechanisms of nutrient cycling (Ellwood and Whitton, 2007; Sundareshwar et al., 2011) or physical flow attenuation in flumes (Larned et al., 2011). Despite extensive research on *D. geminata* in recent years (Whitton et al., 2009), a synthesis of potential ecosystem impacts is still lacking.

Evaluation of ecosystem impacts of an invasive organism is an essential but daunting precursor to quantifying potential economic impacts, or characterizing impacts to ecosystem services (Charles and Dukes, 2007). Together with an understanding of the probability of introduction (Cliff and Campbell, 2012) and secondary spread (Johnson et al., 2001), it could form a more solid basis for a

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management response proportional to valid threats, or aid in the determination of whether action is warranted or feasible. The evaluation of risk (e.g., risk maps, often clamored for in response to the *D. geminata* invasion in Chile) would thus start by defining what thing of value is at risk. However the impacts at the level of the ecosystem are generally more difficult to demonstrate, may vary widely across the range of habitat variability and geographic area, or may be difficult to quantify due to temporal dynamics. Ecosystem studies are generally longer term, may require an advanced stage of invasion in order for effects to be evident, or are otherwise not amenable to the rapid assessment or baseline surveys that characterize field observations during the early stages of invasion.

Our objective is to provide a preliminary assessment of possible ecosystem impacts of *D. geminata* in streams and rivers in Patagonia, a region which presents an additional challenge of having limited baseline characterization. Our primary focus was on potential changes in dominant algal morphologies, standing crop biomass, and fine benthic sediments. Assuming these physical effects are significant, and following recent work on internal mat biogeochemical cycling (Sundareshwar et al., 2011), we evaluated potential secondary effects: potential for abiotic uptake of phosphorous, and the magnitude of interstitial reactive phosphorous and diel interstitial pH dynamics compared to the water column. We also summarize the *D. geminata* literature in order to develop a more general synthesis of known, possible, and probable ecosystem level impacts. Since the magnitude of impacts will likely be greater within a subset of ecological systems, much the same way that

D. geminata blooms occur within a window of physical and biogeochemical conditions (Cullis et al., 2012), we include qualifying observations on the types of water bodies that may be most affected. While our focus is on Chilean Patagonia, this synthesis may also be generally applicable wherever *D. geminata* nuisance blooms have been reported.

2. Methods

2.1. Study sites

We used data from baseline surveys of 39 streams and 87 sites in three major basins in the Aysén region of southern Chile (Fig. 1, Supplementary Table A). Sites were selected based on potential access for recreational or subsistence fishing (e.g., with greater risk of *D. geminata* introduction by human vectors). They are generally characterized as third–seventh order, open canopy, gravel bed rivers of various origin: cordillera (early summer mountain snowmelt regime), pampas (cold steppe, spring snowmelt), glacially influenced (mid summer peak flows and high sediment load), lake outlet or any combination of these (Supplementary Table A). Three rivers, representing the largest most persistent blooms documented in Chile, were the focus of more intensive sampling and experimental studies (Fig. 1). Río Espolón is a third order stream originating from Lago Espolón, with a mean discharge of 63 m^3 s^{-1} (Lobos et al., 1987), and the site of the first documented *D. geminata* bloom for South America in May 2010 (Sarah Spaulding, pers. com.). Río Coyhaique is a third order stream originating in pampas, with a
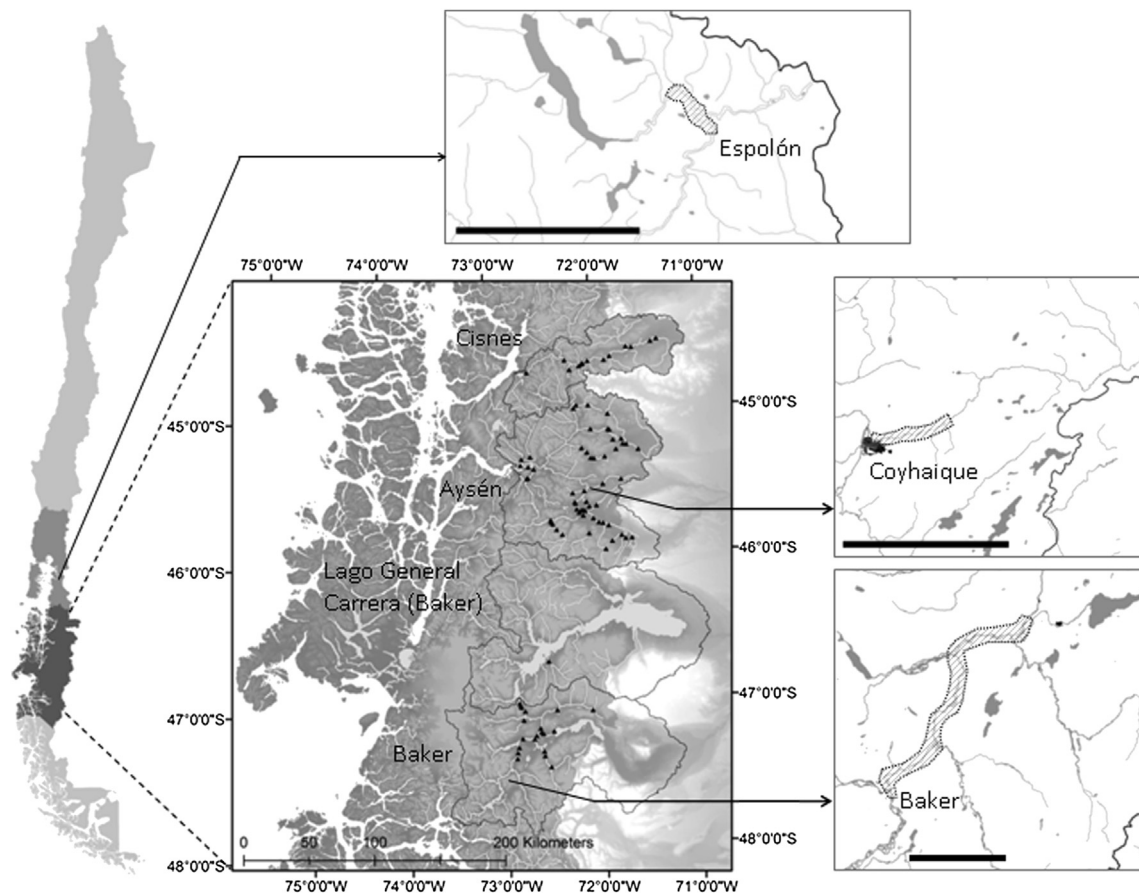

Fig. 1. Map of study area and sampling locations for synoptic surveys (CIEP, 2011), Aysén Region and Palena Province of Chilean Patagonia. Insets show major bloom location and approximate extent (crosshatching) on Río Espolón, Coyhaique, and Baker (Table 2). Black scale bars indicate 20 km.

mean discharge on the order of 10 m^3 s^{-1}; blooms were first documented in November 2010 in a popular bathing area and fishing access in the regional capital of Coyhaique (CIEP, 2011). Río Baker is Chile's largest river, with a mean discharge of 1020 m^3 s^{-1}, originating from the second largest lake in South America (Lago General Carrera/Buenos Aires). The Baker *D. geminata* population extends nearly 70 km (Fig. 1), the most extensive bloom documented for South America, including turbid, glacially influenced waters (suspended sediment ranging from 4.3 to 483 mg L^{-1}, B. Reid, unpubl. data).

2.2. Periphyton characterization, biomass, and associated fine benthic sediment

Visual estimates of algal cover and major periphyton morphologies, and estimates of benthic biomass and associated sediment, were from the 87 reaches sampled between February and April 2011 (Fig. 1, Supplementary Table A). Two parallel longitudinal transects were established in riffle or run reaches at 20 cm and 50 cm depths, 50–100 m downstream of potential points of stream access (areas with high probability of introduction, but below areas of human disturbance). Macroalgal cover along transects, including submersed macrophytes and moss, was visually estimated as Braun–Blanquet cover classes (Bowden et al., 2006), noting presence of major groups: colonial cyanobacteria, filamentous algae (chlorophytes or cyanophytes), mat forming diatoms, submerged vascular macrophytes, and bryophytes. Three stones were selected approximately 10 m apart along each transect, entire stones scraped to remove algal material, and pooled samples were preserved with formalin. Stone surface area was estimated following Biggs and Kilroy (2000).

Samples were homogenized by hand, and a 5–10 ml subsample isolated by sequential centrifugation was retained as reference material and for microscopic determination of the presence of *D. geminata*. The remaining material was dried at 60 °C to constant weight, reweighed, and ashed at 400 °C until constant weight to determine ash-free dry mass (AFDM). Inorganic material was calculated by difference. The contribution of fine mineral sediment to inorganic material was estimated based on a conservative organic matter ash content of 0.4. Ash content of *D. geminata* stalk material (sonicated to remove sediment), filamentous algae (*Ulothrix* sp.), colonial cyanobacterial (*Nostoc* sp.), and moss (*Vittia* sp.), were approximately 0.32, 0.28, 0.25 and 0.15 respectively (B. Reid, unpubl. data). Ash content of benthic organic matter is generally less than 0.2 (McDowell and Fisher, 1976). For sites where biomass was very low (25% of the synoptic sites in Supplementary Table A), organic matter (OM) [g] and fine sediments (S) [g] were estimated volumetrically (v) [cm^{-3}] from the reference material, based on the following relationships derived from local sample material: OM $= 0.0029v^2 - 0.0196v + 0.243$, $n = 31$; S $= 1.30v - 0.369$, $n = 4$.

We analyzed for global difference in standing crop biomass and fine benthic sediments for sites with and without *D. geminata* blooms (Mann–Whitney *U*-test, two independent groups based on sites with and without blooms, using pooled untransformed data from synoptic and bloom surveys). We calculated mean standing crop biomass and fine sediments for each respective morphology, based on sites where only a single primary producer morphology was present. A matrix of relative frequency of co-occurrence of respective pairs of morphological types, based on all sites, was used to evaluate qualitatively the possibility of exclusion of other growth forms by *D. geminata*. We evaluated within-site correlation between organic matter and fine sediments for blooms using linear regression on untransformed data. The global regression model for pooled data from synoptic and bloom surveys was log($x + 1$) transformed. All statistical analyses were performed using Statistica 6.0 (StatSoft Inc.).

2.3. Interstitial phosphorous, abiotic phosphorous uptake, and pH of interstitial mat water

Mat material was sampled from Río Espolón in July 2010, allowing gravity to drain excess water, macroinvertebrates were removed, and mats were transferred to the laboratory. Interstitial mat water was extracted by moderate squeezing, with 50 ml dedicated to analysis of pH, and 50 ml filtered (Millipore nitrocellulose 0.45 μm) and analyzed colorimetrically for soluble reactive phosphorous (SRP, molybdate method, APHA, 2005). pH measurements were performed in a 25 ml closed cell stabilized at 25.0 °C, using a Metrohm 780 pH meter (input resistance $>10^{12}$ Ω, 0.1 mV sensitivity and nominal resolution 0.001 pH units) and a glass combined double junction Ag/AgCl electrode (Metrohm model 6.0257.000). Samples collected over a single 24 h period were analyzed within 1–2 h of field sampling. We also evaluated the abiotic uptake of soluble reactive phosphorous (SRP) by mat material in R. Espolón in July 2010. Mat material was collected as above, and approximately 3 g wet weight was isolated in 50 ml centrifuge tubes ($n = 6$), poisoned with HgCl$_2$, and filtered river water was added to a final volume of 50 ml (mat material occupied the bottom 7–10 cm^3 when immersed). Amendments consisted of ammonium phosphate spiked to a final concentration of 100 μmol L^{-1} P. Controls included untreated *D. geminata* mat ($n = 3$), and P amendment without mat material ($n = 3$). Samples were agitated manually at ambient temperature (5–10 °C) for the first 8 h of incubation. Analysis of soluble reactive phosphorous in the overlying water was conducted following 48 h of incubation. P uptake was evaluated using Mann–Whitney *U*-test (two independent groups, P spike with and without mat). Wilcoxon matched pairs was used to compare interstitial vs. water column SRP and pH: statistical tests for pH were limited to cycle extremes of post dawn (0800–0900 h), mid-day (1100–1400 h) and evening (1700–1800 h) time periods.

2.4. Potential ecosystem effects of D. geminata

We characterized respective *D. geminata* impacts to stream ecosystems as confirmed (based on published peer-reviewed studies), probable (evidence from the gray literature, baseline surveys from South America reported here, or inferred through other published observations), or possible (where evidence and/or studies are lacking). We included an estimation of the types of steam habitat most vulnerable to respective changes in ecosystem function. We use a broad definition of ecosystem impacts, based on six categories of ecosystem processes proposed by Likens (1992) and including an additional category of physical impacts (Simberloff, 2011). In riverine ecosystems this would include effects on transient storage, turbulent flow, hyporheic exchange between ground water and surface water, and sedimentation. We do not address community or biotic interactions, although we recognize the potential role of biodiversity with respect to ecosystem function.

3. Results

3.1. Periphyton characterization, biomass, and trapped fine sediment

Benthic algal and macrophyte communities showed a wide range in standing crop biomass (Fig. 2, Supplementary Table A, Table 1), from below detection (<0.1 g m^{-2})–222.7 g m^{-2}. Fine mineral sediment constituted a high percentage of inorganic material (77% $\pm$ 24). Submersed macrophytes (*Myriophyllum* sp.), the least frequent among the five cover types, had the lowest algal biomass and associated inorganic material, although representative samples were limited. Colonial cyanobacteria (among the most frequent taxa,
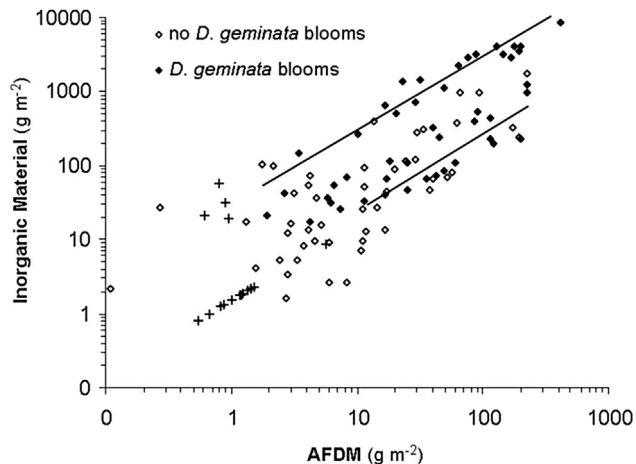
Fig. 2. Relationship between standing crop benthic organic matter (AFDM, primarily algal biomass) and corresponding inorganic material (residual of AFDM, primarily fine mineral sediments). *D. geminata* blooms represented by closed symbols, open symbols show non blooms, and plus signs indicate sites with low biomass estimated volumetrically from reference material (see methods). Data are from the 87 sites in Supplementary Table A, and 31 samples from three *D. geminata* bloom sites (Table 2). Regression lines for Río Baker (above) and Río Coyhaique (below) correspond with data pooled across sampling dates (Table 2).

typically *Nostoc* sp.) and *Rivularia* sp.) were slightly higher at 4.2 g m^{-2} AFDM (range 1.0–11.1). Bryophytes (*Vittia* sp.) and filamentous taxa (*Ulothrix* sp., *Oscillatoria* sp., *Anabaena* sp., filamentous cyanophytes and chlorophytes) were most frequent, and had intermediate values for biomass and inorganic sediments. Two diatom taxa were identified with proliferation of stalk material: the native *Gomphoneis minuta* and the introduced invasive *D. geminata*. Although *Gomphoneis* colonies in general were much more localized than *D. geminata* blooms, the two could not be readily distinguished without microscopic analysis. Stalk-forming diatoms had an intermediate frequency of occurrence, showed the least affinity for other structural groups, and had the highest standing crop biomass and associated trapped inorganic material of any growth form (Table 1). Among the synoptic surveys the overall highest standing crop occurred in mixed assemblages (Table 1, all sites), usually with significant contribution from filamentous algae. When data from synoptic surveys (Supplementary Table A) were pooled with data from major bloom sites (Table 2), standing crop biomass and associated inorganic material were both significantly higher for *D. geminata* blooms (Mann–Whitney U-test, $p < 0.001$). Note that maximum bryophyte, macrophyte and colonial cyanobacteria biomass may be considerably higher for individual stones and microsites.

The relationship between *D. geminata* biomass and fine sediments for major *D. geminata* blooms showed a site-specific linear trend (Fig. 2, Table 2). The relationship was strongest for the turbid, glacially influenced Río Baker, significant across three sample events, and well outside the range of values from baseline surveys. There was no clear relationship for R. Espolón, a lake outlet system, while the regression was significant only for pooled dates for the snowmelt influenced Río Coyhaique. A general regression model across all data had a slightly better fit for log transformed data: $\log(S + 1) = 0.854 \log(OM + 1) + 0.874$, $R^2 = 0.571$, $p < 0.01$, $n = 118$, while the trend for rivers with *D. geminata* blooms could not be distinguished from the overall positive relation between standing crop organic matter and inorganic material (Fig. 2). Estimated contribution of mineral sediments (inorganic residual of AFDM corrected for ash content) was consistently high, approaching 100% for the R. Baker. Inspection of samples confirmed a high concentration of fine mineral sediment trapped within the stalk material, ranging from coarse sands in R. Espolón to fine glacial flour in R. Baker. Low biomass values for R. Baker in November 2012 reflect re-establishment of small *D. geminata* colonies, following extensive scouring from a glacial lake outburst flood on R. de la Colonia, originating from the Northern Patagonia Icefields (B. Reid, pers. obs.).

3.2. Inorganic phosphorous and pH dynamics of interstitial mat water

Soluble reactive phosphorous extracted from *D. geminata* interstitial water (61.5 μg l^{-1}, range 30.4–117.4) was consistently an order of magnitude higher than the corresponding water column at R. Espolón, R. Futaluefú, and R. Noroeste (1.7 μg l^{-1}, range 1.4–7.0, Wilcoxon matched pairs, $p = 0.017$, $n = 7$). Significant abiotic uptake of SRP by mats was also observed (mean uptake 80.7%, sd 0.035, Mann–Whitney U-test, $p = 0.024$). Interstitial water extracted from *D. geminata* mats departed from water column pH over a diel cycle, significantly lower following sunrise (0800–0900 h, mat pH 6.71, sd 0.09, water column pH 7.23, sd 0.03, Wilcoxon matched pairs, $n = 5$, $p = 0.043$), consistently higher during mid-day (1100–01400 h, mat pH 7.66, sd 0.18, water column pH 7.34, sd 0.03, Wilcoxon matched pairs, $n = 3$, $p = 0.11$), and consistently lower at sunset (1700–1800 h, mat pH 7.01, sd 0.09, water column pH 7.36, sd 0.03, Wilcoxon matched pairs, $n = 3$, $p = 0.11$).

3.3. Potential ecosystem effects

The most profound confirmed ecosystem effects are generally mediated through physical changes (biomass, hydrodynamics) and

Table 1

Quantitative estimate of phytobenthic standing crop for major growth forms. Calculations of standing crop organic matter (ash-free dry mass − AFDM), and associated inorganic material (fine sediment and ash content) are based on sites where only a single type was observed macroscopically (*n*). Mixed mat assemblages are included in the "All Sites" category. Overall frequency of occurrence and relative affinity for other types is based on all sites (*n* = 87).

	n	AFDM (g m^{-2})		Inorganic material (g m^{-2})		Affinity (# sites with co-occurrence)					
		Mean	Range	Mean	Range	Freq.	Colon.	Filam.	Stalk	Macro.	Bryo.
All sites	87	20.8	0.0–222.7	111.4	0.0–1747						
Colonial[a]	14	4.2	1.0–11.1	17.5	0.7–101	0.31		12	1	2	7
Filamentous[b]	9	13.0	0.0–56.8	93.0	2.3–284	0.37	12		5	6	13
Stalk/Mat[c]	10	27.1	6.5–65.5	262.7	25.8–1125	0.21	1	5		0	4
Macrophyte[d]	2	2.4	1.8–3.0	8.8	1.2–16.4	0.11	2	6	0		8
Bryophyte[e]	5	12.4	0.3–34.0	101.5	12.9–303	0.28	7	13	4	8	
None	18	4.2	0.0–38.0	31.0	0.0–400.1	0.21					

[a] *Nostoc* sp., *Rivularia* sp.
[b] *Ulothrix* sp., *Anabaena* sp., *Oscillatoria* sp., other.
[c] *Didymosphenia geminata*, *Gomphoneis minuta*.
[d] *Myriophyllum* sp.
[e] *Vittia* sp.

Table 2
Interaction between algal standing crop biomass and benthic fine sediment deposition for lake outlet, pampas, cordilleran and glacially influenced systems dominated by *D. geminata*. Ranges shown for AFDM and inorganic material, while the percentage of mineral sediment contribution to inorganic material was estimated assuming an organic matter ash content of 0.4 (see text). Beta coefficients shown for linear regression models, significant relationships in bold.

Site	Type	Date	AFDM (g m^{-2})	Inorg. (g m^{-2})	% Sed.	n	R^2	β	p
R. Espolon	Lake Outlet/Cordillera	30-Apr-11	20.7–91.6	237.9–540.3	90.2 (±4.5)	5	0.134	n.s.	0.544
R. Coyhaique	Pampas	24-Nov-10	114.4–223.2	227.2–1221	66.1 (±16.1)	5	0.354	n.s.	0.29
		22-Mar-11	3.6–77.3	17.3–168.0	72.8 (±19.0)	8	0.346	n.s.	0.07
		All				13	0.68	0.841	**<0.001**
R. Baker	Lake Outlet/Glacial	21-Oct-11	3.4–130.8	147.2–4072	98.4 (±0.4)	6	0.96	0.984	**<0.001**
		3-Dec-11	147.3–410.1	2894–8700	96.7 (±0.3)	6	0.971	0.988	**<0.001**
		21-Nov-12	1.9–63.6	21.1–2229	96.8 (±1.7)	6	0.968	0.987	**<0.001**
		All				18	0.925	0.964	**<0.001**

biogeochemical processes within *D. geminata* mats (Table 3). The two categories are not independent, hydrodynamic effects potentially playing a significant role in solute exchange and transient storage, in turn potentially affecting benthic biomass, feeding back to more enhanced hydrodynamic effects. In both cases the magnitude of effects to whole stream ecosystems depends on stream bed coverage and longitudinal extent of *D. geminata* blooms, together with physical characteristics such as geomorphology and water velocity (determines the exposure to reactive surface areas, Ensign and Doyle, 2006) and turbulence (drives gas exchange, and hence moderates the effects of dissolved oxygen or inorganic carbon depletion). In short, smaller less turbulent headwater streams, such as those that originate from the pampas, may be at greater risk of ecosystem impacts. Note that *D. geminata* blooms in upstream areas may also be a symptom of more advanced state of invasion (Kilroy and Unwin, 2011). Ecosystem effects on whole stream pH, dissolved oxygen (stream metabolism), or nutrient spiraling, have yet to appear among the growing body of investigations on *D. geminata* blooms. One of the seven general categories in Table 3 has not apparently been addressed in any form: resistance and stability (resilience) of *D. geminata* associated biotic communities (e.g., Grimm and Fisher, 1989). A change in primary producer stability may vary spatially, seasonally and among years, due to potential *D. geminata* resistance to spates (Larned et al., 2011; Cullis et al., 2012), or from dramatic changes in benthic structure when the critical shear stress is exceeded.

4. Discussion

4.1. Potential for biogeochemical state change in Patagonian streams

Sediment trapping by *D. geminata* mats is mentioned by a number of authors, usually in the context of particulate organic matter (Kirkwood et al., 2007; Larned et al., 2011). The variation in algae-associated sediment across macroalgal morphologies in baseline surveys in Chile (Fig. 2) provides a general correlation between algal biomass and accumulation of inorganic matter (which is mostly fine mineral sediment). Two of the major *D. geminata* populations bracket the range of biomass–sediment distribution, an indication that the determining factors in sediment accumulation may be site specific (the intercept of the regression lines in Table 2), depending on riverine suspended sediment or bedload, local geomorphology, and timing and intensity of recent spates with respect to bloom development (within-site variation across dates in Table 2). Nevertheless, based on the general conformity of slopes of the bloom regressions compared to the global relationship (Fig. 2), it cannot be argued that *D. geminata* is more efficient at trapping sediments, only that it results in enhanced sediment trapping through greatly increased organic biomass, especially in systems where substantial biomass would not normally accumulate under oligotrophic conditions.

Observations on R. Baker suggest the potential biogeochemical importance of sediment trapping; the largest continuous *D. geminata* bloom documented from South America also had the highest recorded values for biomass and benthic sediments (AFDM values for the Baker approached those reported for nuisance blooms in New Zealand; Kilroy et al., 2009). The strong linear relationship between *D. geminata* biomass and associated sediment occurs in a system with stable flow (due to the influence of South America's second largest natural lake) and with continuous suspended sediment load. Fine mineral sediments may be very reactive, particularly in the case of glacial flour, increasing reactive and sorptive surface, providing substrate for microbes, and contributing trace ions through mineral weathering. However the massive blooms in a turbid glacial river (post-flood colony formation observed at 0.5–0.7+ m depths, with light extinction k_d approximately 1.6–2.7 m^{-1}, unpubl. data) conflict with previous studies on light limitation of cell and stalk production (Kilroy and Bothwell, 2011), and preferential bloom formation in low turbidity or non-glaciated environments (Kirkwood et al., 2007; Kilroy et al., 2008). We note that the light environment for *D. geminata* is still not adequately characterized (PAR$_c$, Cullis et al., 2012). Extreme sites such as R. Baker provide an opportunity to better define the overall *D. geminata* niche (Cullis et al., 2012). We cannot discard the possibility that within this niche, the impediment from a reduced light environment might be offset by biogeochemical advantage of fine sediment accumulation.

Particle trapping may contribute to secondary effects of *D. geminata* mat development. We observed significant abiotic phosphorous uptake, together with interstitial soluble reactive phosphorous concentrations an order of magnitude higher than in the water column, indicating potentially significant phosphorous scavenging under oligotrophic conditions. Direct comparison between this study and experimental phosphorous uptake studies from North America (Sundareshwar et al., 2011) is confounded by differences in methods (analysis via digestion, and much greater P amendment). Extraction of interstitial water may result in lysing of cells or metazoans, although molybdate staining of stalk material confirms the high concentration of reactive phosphorous (unpubl. data). With respect to abiotic phosphorous uptake, it is not possible to distinguish between the effects of stalk material and mineral sediments without additional physical separation. Nevertheless, our observations validate the possibility that newly documented South American *D. geminata* population conforms to known effects of *D. geminata* blooms elsewhere.

The compelling model for capture and internal recycling of phosphorous proposed by Sundareshwar et al. (2011) suggests a steady state mechanism. Our observations of a 0.7 log unit daily variation of internal mat pH (strong gradients within the mat may

Table 3
Summary of confirmed (C), probable (Pr) or possible (Po) ecosystem impacts of D. geminata in streams and rivers.

Ecosystem function	Indicator	Effect	Vulnerability
1. Biomass	a. Primary Producer Biomass	Increase (Pr — based on Chlorophyll concentration or cell density)[1,2]	Oligotrophic streams
	b. Organic Matter Standing Crop	Order of magnitude increase in polysaccharide stalks (C),[1,3] sedimentation of particulate organic matter (Pr)[2,5]	Non-forested autotrophic systems
2. Productivity	a. Chlorophyll	Increase (C)[1]	Oligotrophic streams
	b. Dissolved Oxygen	Increased diel cycling and dark respiration (Pr — extreme super-saturation and steep vertical dissolved oxygen profiles)[4]	Less turbulent reaches in small streams
	c. pH	Enhanced diel cycle of whole stream pH (Pr — based on internal mat diel cycle)[5]	Poorly buffered, carbon limited small streams
3. Energy Flow	a. Decomposition	Increased proportion of organic matter resistant to decomposition (Pr)[6]	Heterotrophic streams
	b. Trophic Structure	Increased importance of microbial heterotrophic production and microbial loop (Po), change in functional feeding groups and decrease in grazers (Po)[7,8]	
	c. Organic Matter Drift	Increased episodic organic matter subsidy downstream following flood events (Po)	
	d. Secondary Production	Increased dominance by small size class invertebrates (C),[1,9] decreased invertebrate turnover time (Pr), increased respiration and P/B ratio (Pr), change in invertebrate production (Po) or fish production (Po — depending on feeding selectivity, energy return on investment, terrestrial vs. aquatic sources)	
4. Nutrient Cycling	a. Uptake/Spiraling	Increased sorptive surface area on stalks (Po),[10]	Small streams
	b. Nitrogen Fixation	increased rates of uptake of cations (Pr),[11] secondary sorption of inorganic P (Pr) and organic nutrients (Po)[5,11,12]	
	c. Diel Cycling	Displacement of native N-fixing Cyanobacteria (Po)[5]	Patagonian and possibly austral streams
		Increased amplitude in diel concentration of metals in the water column (Po — based on pH and DO cycling)	Small streams
5. Resilience/Stability	a. Macroinvertebrate Community Stability	Increase (see 7e) or decrease due to episodic removal of structure forming DG biomass (Po)	
	b. Periphyton Community Stability	Increase (see 7e) or decrease due to episodic removal of DG biomass (Po)	
6. Development	a. Periphyton Succession	Change in succession sequence mediated by stalk development (Pr),[13,14] reduced epilithic diatoms and cyanobacteria (Pr)[5,13,14] later dominance of filamentous algae on senescent mats (Po)	
	b. Microbial Succession	Increased sulfate and iron reducing bacteria (C),[11] increase in other microaerophilic or anaerobic microbes (Pr)	
	c. Invertebrate Succession	Increased habitat structure facilitating selective colonization within the DG mat (Po)[1]	
7. Physical Engineering	a. Transient Storage	Increased water residence time in the benthic algal mat (Pr),[4] increased column-mat solute exchange (Pr)[4]	Fast flowing turbulent streams
	b. Turbulence	Decreased near bed turbulence (C),[4] increased shear stress above mats (C)[4]	Fast flowing turbulent streams
	c. Hyporheic Exchange	Decrease in local vertical hydraulic conductivity, local physicochemical effects on trout redds (Po)[15]	Alluvial streams
	d. Sediment Dynamics	Increased sediment retention (Pr)[2,5]	Systems with sediment loading
	e. Bed Stability	Higher flow rate for critical shear stress bed disturbance (Pr)[16]	Small streams with continuous coverage

References: [1]Kilroy et al., 2009, [2]Kirkwood et al., 2007, [3]Kilroy and Bothwell, 2011, [4]Larned et al., 2011, [5]this study, [6]Gretz, 2008, [7]Rost et al., 2008, [8]James et al., 2010, [9]Gillis and Chalifour, 2010, [10]Aboal et al., 2012, [11]Sundareshwar et al., 2011, [12]Ellwood and Whitton, 2007, [13]Hoagland et al., 1982, [14]Floder and Kilroy, 2009, [15]Bickel and Closs, 2008, [16]Cullis et al., 2012.

result in significantly greater pH extremes) hints at a more dynamic mechanism for biogeochemical processes in *D. geminata* mats. Strong internal pH fluctuations, driven by respiration of CO_2 and probably corresponding with dissolved oxygen diel cycling (i.e. the strong oxygen gradient observed by Larned et al., 2011) and redox condition, would affect most chemical and biological processes including redox reactions, microbial community composition, chemical kinetics and abiotic sorption within the *D. geminata* mat community. The boundary between oxidized and reduced conditions (Fig. 2 in Sundareshwar et al., 2011) may move, thus providing

a mechanism for complexation and liberation of nutrients and other resources over daily time scales. Such a mechanism observed in subsurface geochemistry has been aptly termed a "redox pump" (Moore, 1994). Another consequence of strong pH cycles within *D. geminata* mats is the potential effect on phosphatase enzymes at the base of the *D. geminata* stalk (Ellwood and Whitton, 2007; Whitton et al., 2009). These enzymes are active under alkaline conditions, however our results indicate that pH buffering within the mat (speculated by Ellwood and Whitton, 2007) is unlikely, but that large diel swings (due to high respiration rates in more

mesotrophic systems, or higher temperature) may inhibit/activate these enzymes at low/high pH respectively. This corresponds with the limited occurrence of *D. geminata* blooms in pH < 7 (Beltrami et al., 2008; Kilroy et al., 2008; Reid et al., 2012).

The presumption of biogeochemical impacts on stream ecosystems hinges on the interpretation of three alternative hypothesis regarding the source and role of nutrients in *D. geminata* cell division and stalk production. Ellwood and Whitton (2007) observed high alkaline phosphatase activity at the junction between *D. geminata* cells and stalk, reasoning that *D. geminata* may efficiently process organic forms of phosphorous. Sundareshwar et al. (2011) proposed a more comprehensive interaction between iron, sulfide, organic matter and phosphorous, together with a dynamic mechanism of adsorption and complexation depending on variable reducing conditions within the polysaccharide mat. Meanwhile, Kilroy and Bothwell (2011, 2012) offer a more simple explanation, strongly supported by experimental amendments, of increased cell division when SRP is available and increased investment in stalk production during phosphorous limitation. Their experimental increase in stalk length by a factor of 2.5–4 is compelling, but does not quite explain increases in benthic biomass (which could have a variety of origins) under field conditions (e.g., the 10–185 fold increase reported by Kilroy et al., 2009). Competing explanations for the paradox of bloom formation in oligotrophic waters border on polemic (e.g., Bothwell et al., 2012). However the three hypotheses are not mutually exclusive, to date none have been totally falsified, and perhaps all have some common ground in contributing toward an understanding of ecosystem impacts on stream biogeochemical cycling. Regardless of the proximal factors that regulate *D. geminata* blooms or confer resistance to invasion, evidence points to the formation of strong biogeochemical gradients and dynamic biogeochemical cycling, which might be considered biogeochemical hot spots (*sensu* McClain et al., 2003; Cullis et al., 2012).

In comparison, native benthic algal communities in Patagonian streams may be characterized by a significant component of nitrogen-fixing cyanobacteria, mixed macrophyte communities, or lower, visually undetectable benthic algal biomass. The high frequency of cyanobacteria is not surprising given the low inorganic nitrogen in Patagonian streams (Perakis and Hedin, 2002). That the genus is not included in a recent review of the principal genera known from Chilean continental waters (Parra, 2006) is more than anything an indication of a limited sampling and baseline knowledge of stream ecosystems in the region. In contrast, communities dominated by the stalk-forming *D. geminata* have over an order of magnitude higher standing crop biomass than native communities, with corresponding increase in fine benthic sediments. Additionally, *D. geminata* communities have the potential for biogeochemical changes due to scavenging of phosphorous despite oligotrophic conditions, and producing more intense daily pH cycling in the mat and possibly the water column. The unusually extensive *D. geminata* bloom in a turbid glacial river may be an indication of future invasion into novel habitats, accumulation of periphyton biomass, organic matter and mineral sediments resembling a form of pedogenesis in the benthic zone of rivers. The potential for displacement of native nitrogen-fixing communities by an efficient phosphorous scavenger that can modify hydrodynamic conditions, biogeochemistry and sedimentation, represents a potential state change for stream nutrient cycling and stream ecosystem function in Patagonia.

4.2. Effects on ecosystem services: global perspective

Several potential ecosystem impacts of *D. geminata* blooms may translate into quantifiable negative economic impacts. For example

a decrease in dissolved oxygen concentration or significant changes in pH might directly or indirectly result in impaired water quality. However given the observations summarized in Sections 4.1 and 4.2, any drastic change in these two parameters may be self-limiting in terms of persistence of *D. geminata* blooms, especially in smaller streams. Despite numerous references to possible decline in dissolved oxygen from online web-based sources or literature intended for the general public, such claims probably originate from the general confusion between eutrophication and *D. geminata* blooms, which is not associated with eutrophic conditions. Meanwhile, the potentially significant impacts of *D. geminata* blooms on native ecosystems through changes in physical, biogeochemical and functional diversity (Sections 4.1 and 4.2) do not lend themselves to a quantitative economic assessment.

Effects on fish production (3d, Table 3) have been a preoccupation since the first documented *D. geminata* nuisance blooms. In Patagonia a distinction must be drawn between native fish (which are poorly known) and introduced trout and salmon (which are also poorly quantified but are more readily recognized for their recreational value). Aesthetic impacts via high periphyton biomass (1a), decay resistance of the biomass (3a), and episodic drift of periphyton that might interfere with angling (3c), are all possible but similarly difficult to demonstrate without data on recreational use, psychological effects and change in recreation behavior, and potential loss of indirect economic subsidies in the tourism sectors (Beville et al., 2012). Actual impacts on fish production may be possible under certain circumstances, such as the reported decline of brown trout populations together with the initiation of nuisance blooms in Rapid Creek South Dakota (Larson and Carreiro, 2008). However these authors also caution that the decline corresponded with drought induced reduction in stream flow. Populations of Chum, Coho and Steelhead in British Columbian rivers with *D. geminata* blooms showed increased spawners and production in some rivers, while no effect was observed in other rivers (Bothwell et al., 2008). Nearly a century of documented blooms in Norway coincides with two of the most productive salmon rivers (Lindstrøm and Skulberg, 2008), and the authors suggest that fisheries management represents a far graver threat to wild salmon production. Jonsson et al. (2008) report that pre- and post-invasion electrofishing surveys in River Hvítá in Iceland did not demonstrate any obvious effect from high density *D. geminata* on juvenile salmon abundance. Whole system energetics and food web analysis (Huryn, 1996), rarely conducted but certainly feasible given advances in recent decades, may be needed in order to resolve potential impacts of *D. geminata* on fish production isolated from other potential factors. On a more practical level, the perceived negative effects of *D. geminata* on fish may be conflated with limited management of recreational fisheries. In Patagonia the prized trout and salmon, all of which are introduced species, may also be attributed to largely unchecked subsistence fishing (B. Reid, pers. obs.). The invader becomes a scapegoat, while more comprehensive policies and on-the-ground management, with a solid foundation in ecosystem dynamics in continental waters, might not be properly considered.

Our assessment of the ecosystem impacts of *D. geminata* invasion in streams demonstrates the potential effects across all categories of ecosystem function. However, there are many aspects of the effects on ecosystem function that despite almost a decade of research are still poorly known. Many of the predictions on biogeochemical impacts are based on inference, while effects on fish (which motivates much of the public response to *D. geminata* invasion) are still unclear. The paradox of needing more sophisticated and time consuming field studies to understand ecosystem impacts of an invading organism represents a challenge for invasive species management. This is especially true for one of few recognized algal or microbial invaders (Floder and Kilroy, 2009), narrowing the

distinction between the spread of invasive species and infectious disease (Crowl et al., 2008). Considering the short generation time and hence potentially reduced lag time in the invasion, the strategies necessary for control, prevention and/or elimination may differ from the typical target invasive (Reid et al., 2012), and eradication may not ever be possible (Floder and Kilroy, 2009). It also may underscore the unavoidability of comprehensive global biosecurity measures in continental waters, to be better able to prevent initial introduction of *D. geminata* and other potentially harmful aquatic microorganisms, such as whirling disease (*Myxobolus cerebralis*) and chytrid fungus (*Batrachochytrium dendrobatidis*).

5. Conclusions

The Patagonian invasion by the diatom *D. geminata* represents a distinct challenge compared to other regions: not only are affected systems poorly characterized, but also a general understanding of the mechanisms and magnitude of ecosystem level impacts of *D. geminata* is still lacking. This places a strong limitation on characterizing and quantifying the effects of an invasive organism on various ecosystem services, which in turn determines the focus and extent of the management response. The most profound confirmed ecosystem effects of *D. geminata* are generally mediated through physical changes (substantially increased algal biomass, sediment trapping, and altered hydrodynamics) and biogeochemical processes (pH, phosphorus uptake) within *D. geminata* mats, and the two categories are probably interdependent. The combination of characteristics of *D. geminata* blooms, as a dominant and aggressive stalk-forming diatom, the potential for efficient scavenging of phosphorous despite oligotrophic conditions, more intense daily pH cycling in the *D. geminata* mat and possibly the water column, and efficient trapping of suspended sediments, is in sharp contrast to current conditions characterized by a significant component of nitrogen-fixing cyanobacteria in mixed macrophyte communities. Given the considerable investment in monitoring and management of the *D. geminata* invasion, first in New Zealand and more recently in South America, efforts to contain or mitigate for *D. geminata* invasion and nuisance blooms may be a justifiable management investment, but not necessarily for the stated reasons.

Acknowledgments

Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.actao.2013.05.003.

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