A conceptual model for the blooming behavior and persistence of the benthic mat-forming diatom *Didymosphenia geminata* in oligotrophic streams

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[1]   The benthic, mat-forming diatom *Didymosphenia geminata* has the unique ability to produce large amounts of algal biomass under oligotrophic conditions in cold, fast flowing streams and rivers. This presents an ecological paradox that challenges our current understanding of stream ecosystem dynamics. Our understanding of the drivers of *D. geminata* ecology is still limited. Here we present a conceptual model for the blooming behavior and persistence of this species to advance scientific understanding of strategies for life in fast flowing oligotrophic waters and support the design of future research and mitigation measures for nuisance algal blooms. The conceptual model is based on a synthesis of data and ideas from a range of disciplines including hydrology, geomorphology, biogeochemistry, and ecology. The conceptual model highlights the role of water chemistry, river morphology, and flow thresholds in defining the habitat window for *D. geminata.* We propose that bed disturbance is a primary control on accumulation and persistence of *D. geminata* and that the removal threshold can be determined by synthesizing site-specific information on hydrology and geomorphology. Further, we propose that a key to understanding the didymo paradox is the separation of cellular reproduction and mat morphology with specific controls acting in respect of the different processes.

1.   Introduction

[2]   The functioning of stream ecosystems is maintained through a diversity of biotic and abiotic controls [*Allan and Castillo*, 2007] and complex physical and biological interactions [*Hart and Finelli*, 1999]. Improving our understanding of the complexity of natural systems requires a synthesis of observations, theories, methods and perspectives drawn from diverse fields [*Harte*, 2002]. Our understanding is also challenged by issues of scale and requires us to find ways to bridge the gap between observations of physical, chemical, and biological processes at small scales and observations of ecological outcomes at large scales in complex, dynamic, and highly nonlinear environmental systems [*Rundle et al.*, 2006]. This synthesis of ideas and understanding is important to better understand the functioning of these systems, and also to improve predictability and our ability to anticipate, and where possible mitigate, the consequences of adverse natural and human induced changes [*Hubbard and Hornberger*, 2006].

[3]   The mat forming diatom *Didymosphenia geminata* (Lyngbye) M. Schmidt is growing in significance in its impact on lotic systems globally [*Blanco and Ector*, 2009]. This organism presents an ecological paradox, that challenges our understanding of fundamental processes in stream ecosystems as it has the apparently unique ability to rapidly produce large blooms of algal biomass under very low nutrient (oligotrophic) conditions in the high-shear, highly turbulent environments of mountain streams [*Kirkwood et al.*, 2007]. We term this the didymo paradox. The explanation for this paradox is unclear but it is likely to involve aspects of ecology, hydrology, biogeochemistry and geomorphology. It therefore presents a unique opportunity to investigate the role of synthesis in understanding the complex interactions and processes in an environmental system.

[4]   The objective of this paper is to present a conceptual model for the growth, persistence and blooming behavior of

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D. geminata in respect of the didymo paradox. Current understanding and data on the specific habitat requirements for this organism are limited [*Whitton et al.*, 2009]. The aims of developing a conceptual model are to synthesize current understanding and existing research, describe particular areas of uncertainty that require further investigation, and identify data that could be used to test current hypotheses on physiological traits and environmental conditions that promote nuisance blooms. The development of a conceptual model is also the first step in developing a mechanistic model for this species that can be used to test specific research hypotheses on the dynamics of stream ecosystems and to evaluate possible mitigation measures for nuisance algal blooms.

2. Background

2.1. Threat to the Sustainability of Stream Ecosystems

[5] *Didymosphenia geminata* is a benthic mat forming diatom that is increasing in significance as a nuisance species in freshwater streams throughout the United States, Europe and Asia [*Blanco and Ector*, 2009]. *D. geminata* cells are attached to the stream substrate by an extracellular polysaccharide stalk [*Gretz*, 2008] produced at an apical pore field at the foot of the cell. Over time the stalks lengthen and branch when the cell divides. The result is a dense algal mat that can be up to a few centimeters thick and cover extensive portions of the streambed. *D. geminata* mats significantly impact the aesthetic appeal of the stream [*Spaulding and Elwell*, 2007] and habitat structure, and foodweb dynamics [*Gillis and Chalifour*, 2010; *Kilroy et al.*, 2009]. This has potentially significant ecological as well as economic implications for tourism, recreational use, fly fishing, and commercial fisheries. Thick algal mats growing in the stream or dislodged during periods of high flow can also clog intakes for water treatment works and reduce the conveyance efficiency of irrigation or hydroelectric canals, resulting in expensive clearing work.

2.2. Increasing Global Concern

[6] Samples from lake sediments in Alaska show that *D. geminata* blooms have been part of the natural system in northern latitudes for many thousands of years [*Pite et al.*, 2009]. Periodic blooms have also been observed in the past in parts of Northern Europe [*Blanco and Ector*, 2009]. In recent decades, however, there has been an apparent increase in the occurrence of nuisance blooms in its traditional habitats of North America, Europe and Asia as well as expansion into new watersheds [*Spaulding and Elwell*, 2007]. In 1989 concerns were first raised about *D. geminata* blooms forming in rivers on Vancouver Island [*Bothwell et al.*, 2009]. These were followed by increasing concerns about blooms in streams in Europe [*Kawecka and Sanecki*, 2003], Asia [*Bhatt et al.*, 2008] the U.S. [*Bergey et al.*, 2009; *DePalma*, 2009; *Miller et al.*, 2009] and Canada [*Kirkwood et al.*, 2008]. In 2004 *D. geminata* invaded streams in the South Island of New Zealand and spread quickly to most watersheds on the South Island [*Kilroy and Unwin*, 2011]. The impact on streams in New Zealand was so dramatic that it raised the global awareness of the potential for aesthetic and ecological impacts of nuisance algal blooms in flowing waters [*Bothwell and Spaulding*, 2008; *Spaulding and Elwell*, 2007]. This sparked a major public awareness and prevention campaign

in New Zealand with *D. geminata* being officially declared an "unwanted organism" [*Vieglais*, 2008]. In 2010 *D. geminata* blooms were confirmed for the first time in South America [*Segura*, 2011]. Globally *D. geminata* is acknowledged to be one of the most problematic invasive species currently threatening lotic systems [*Blanco and Ector*, 2009].

2.3. The Didymo Paradox

[7] *D. geminata* is unusual in that it is the only known freshwater diatom to produce nuisance blooms. These blooms appear to grow best under low temperature and low nutrient (oligotrophic) conditions in fast flowing, highly turbulent streams [*Spaulding and Elwell*, 2007]. The growth of benthic algae is typically favored by increasing concentrations of dissolved nitrogen and phosphorus [*Dodds et al.*, 2002]. Nuisance and harmful algal blooms are often the result of natural and man-made increases in these nutrients, and are typically observed in warm water lakes, large rivers, estuaries and the ocean [*Anderson et al.*, 2002; *Herath*, 1997; *Smith et al.*, 1999]. *D. geminata* therefore presents an ecological paradox that challenges our current understanding of stream ecosystem functioning [*Kirkwood et al.*, 2007]: how can so much biomass be produced so quickly under such low nutrient conditions and persist in these high shear environments? Here we present a conceptual model focused on the role of threshold dynamics, habitat windows, and the separation of cellular and mat forming controls that addresses this paradox and provides insights into the complex dynamics and physical and biological coupling in stream ecosystems.

3. Outlining a Conceptual Model Based on Threshold Dynamics

[8] The study of thresholds and corresponding pattern dynamics has been proposed as an option for bridging the gap between observations of small-scale processes and large-scale outcomes in complex, highly nonlinear environmental systems [*Rundle et al.*, 2006]. The study of threshold dynamics and how these vary in space and time can be used not only to predict the likely state of the system, but response functions define by specific ecological threshold can also lead to extremely high reaction and growth rates at particular locations or times yielding hot spots and hot moments of biological activity [*McClain et al.*, 2003]. The period blooming tendency of *D. geminata* represents such hot moments of biological activity and hot spots are determined by the spatial distribution of these blooms both within a watershed and between watersheds. The spatial and temporal dynamics of *D. geminata* blooms are therefore potentially controlled by some as yet undefined critical threshold response to changing environmental conditions.

[9] A fundamental concept behind threshold behavior is that there are distinct modes of dynamic behavior at the macro-scale [*Zehe and Sivapalan*, 2009]. The response of a system therefore is determined not only by the boundary conditions (e.g., abiotic factors such as nutrients, light and temperature for an ecological system), but also by internal thresholds determined by the system properties (e.g., a removal threshold or minimum light requirement for specific species) and the initial state of the system (e.g., low biomass following a removal event resulting in historical effects) [*Zehe and Sivapalan*, 2009]. Consideration of the different
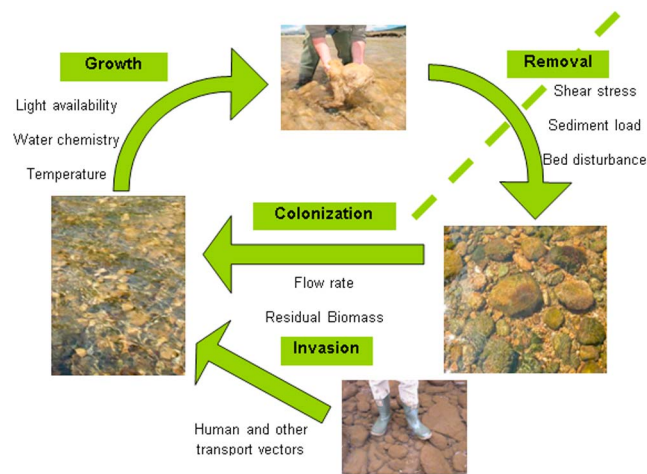
Figure 1. Proposed dynamic phases (in bold) for modeling the growth dynamics of *D. geminata* and the potentially significant controlling parameters for each dynamic phase.

dynamic states of *D. geminata* ecology in a conceptual model for the growth, persistence and blooming behavior of this nuisance species are outlined in Figure 1. Here it is important to note that the factors controlling the response of the organism in each dynamic state are distinct from the critical thresholds that define the different states. The four dynamic states identified in Figure 1 are the initial invasion, growth or invasive response, removal due to some disturbance event, and recovery and recolonization following the disturbance event. These different dynamic states are separated by hydrologic and other events that potentially trigger a threshold response changing from one dynamic state to another. The response of the organism within each of these different dynamic states is then controlled by a range of interacting variables as shown in Figure 1 that involve linear as well as highly nonlinear response functions.

[10] In highly dynamic systems such as streams and rivers, the movement between different dynamic states for the growth of benthic algae is controlled primarily by seasonal variations in flow, temperature and light [*Lewis and McCutchan*, 2010]. Of these, flow variations is considered to be the master variable [*Poff et al.*, 1997]. Figure 2 shows how a range of critical flow thresholds can be used to define the dynamic states of *D. geminata* life history. These include phases of growth and no growth (due to the impact of flow rate on limiting the penetration of light to the streambed), removal due to a flow flow-related disturbance event, and recolonization after the disturbance event. Although Figure 2 highlights the importance of variations in flow in determining the transition between these dynamic states, seasonal variations in other controlling variables such as temperature, light and water chemistry may potentially also be significant.

4. Invasion and Growth Defined by a Suitable Habitat Window

[11] Initial colonization or invasion is clearly a primary threshold event. Like other aquatic species, *D. geminata* cells are transported not only by water flow but also be numerous other vectors. If conditions are favorable (i.e., cool and

damp), individual cells can survive for extended periods of time outside of the stream environment [*Kilroy et al.*, 2007] allowing the diatom to re-establish colonies after droughts or removal events, and to establish new colonies when transported to new streams.

[12] There are many possible ways in which human activities are likely to have played a role in the spread of *D. geminata* to new watersheds [*Kilroy and Unwin*, 2011]. The first documented nuisance blooms of *D. geminata* in North America occurred at popular fishing sites along rivers on Vancouver Island [*Bothwell et al.*, 2009]. These blooms followed a significant increase in recreational fishing and the rise in popularity of felt-soled wading boots. Felt-soled waders are a major concern as cells can potentially remain viable for many weeks in the damp conditions provided by the felt sole [*Kilroy et al.*, 2007]. They have also been shown to be a significant vector in the transport of other aquatic nuisance species such as whirling disease [*Gates et al.*, 2008] and New Zealand mud snails (see http://www.anstaskforce. gov/Documents/NZMS_MgmtControl_Final.pdf).

[13] While the occurrence of *D. geminata* in new watersheds can be attributed to the introduction of cells by human vectors, the immigration of a new species is not sufficient to result in survival or a successful invasion [*Mack et al.*, 2000]. The success of the initial colonization of *D. geminata* and the potential for future blooms is clearly defined not only by the introduction of cells, but also by a suitable habitat window for survival. Equally there is likely to be some genetic underpinning that determines not only the potential for survival, but also the tendency to form nuisance blooms as shown by the inner habitat window in Figure 3.

[14] Neither the parameters defining the habitat window for the survival and tendency to bloom of *D. geminata* nor the critical values of these defining parameters have been fully identified. Like other aquatic organisms, the survival and proliferation of *D. geminata* in a particular stream is influenced by the interaction of a variety of landscape features that act as environmental filters [*Poff*, 1997]. Studies of the spatial and temporal patterns of distribution of *D. geminata* suggest a range of potential controls that could define a suitable
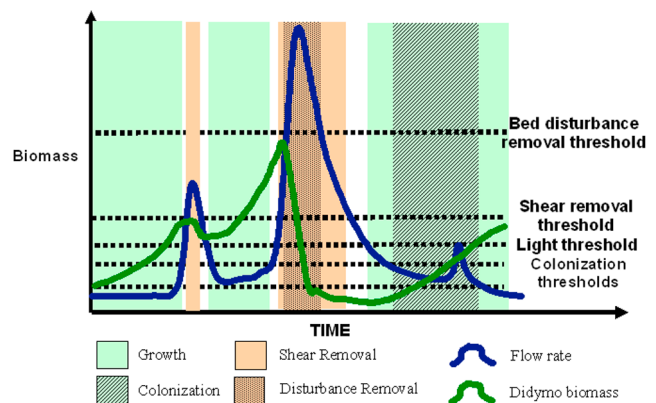

Figure 2. Schematic representation of the relationship of various thresholds that may affect *D. geminata* mat growth/ biomass under variable flow. Thresholds are ordered from lower flow (colonization thresholds, bottom) to higher flow (bed disturbance removal threshold, top).
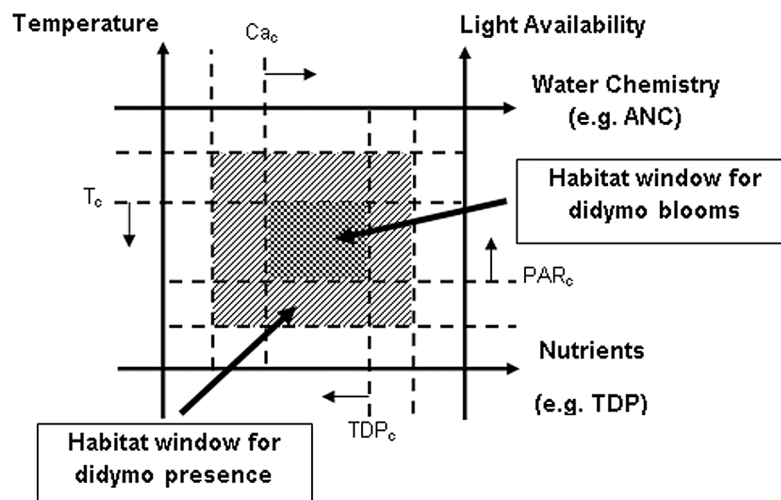
Figure 3. Example of a proposed habitat window describing the potential for *D. geminata* to be present in a stream as well as the potential for nuisance blooms to form, as defined by a set of as yet unconfirmed and unknown potential critical threshold requirements for temperature (T_c), light availability (PAR_c), water chemistry represented by acid neutralizing capacity (ANC_c), and nutrient concentrations (TDP_c).

habitat window. These include high light availability [*Whitton et al.*, 2009], low nutrient concentrations [*Spaulding and Elwell*, 2007], low temperatures [*Kumar et al.*, 2009], and specific water chemistry thresholds [*Rost et al.*, 2011]. These are likely controlled by local climate as well as specific characteristics of the river catchment, including watershed morphology, the terrestrial ecosystem surrounding the stream, and the underlying geology and groundwater flow system. Determining the critical threshold values that define the habitat window for nuisance blooms is vital for identifying streams at risk as well as for predicting the likelihood of future nuisance blooms, and should therefore be a key focus of future research efforts. Consideration of the potential parameters and critical threshold values of these parameters defining the habitat window for *D. geminata* will be discussed in later sections. Potential candidates for the critical threshold parameters for both presence and blooming potential of *D. geminata* are critical light availability in terms of Photosynthetically Active Radiation (PAR_c), critical nutrient concentration such as total dissolved phosphorus (TDP_c), critical water chemistry characteristics such as Acid Neutralizing Capacity (ANC_c) and critical temperature thresholds (T_c) as shown in Figure 3.

5. Shear Stress, Bed Disturbance, and the Scouring of Mats

[15] There are many factors controlling the dynamics of stream ecosystems, but the removal due to high flow events is considered to be one of the primary regulators particularly in very dynamic streams and rivers [*Biggs et al.*, 1999]. The removal of benthic algal is often defined in terms of a critical flow rate as flow is the most readily available hydraulic parameter [*Poff and Ward*, 1989]. Variations in bulk discharge are not always sufficient to explain the dynamics of stream ecosystems as it is rather the specific hydraulic parameters such as depth, velocity, shear stress and bed disturbance that are relevant to aquatic organisms [*Townsend*

et al., 1997]. These flow habitat features can vary significantly between sites for the same flow rate, and even within a single stream reach, and at different times of the year due to variations in channel morphology and the influence of previous events and condition of the benthic ecology [*Biggs et al.*, 1999].

[16] The primary mechanisms for the removal of benthic algae are hydrodynamic forces exerted on the organism itself (lift and drag), abrasion due to suspended particles, and scouring resulting from disturbance of the substrate [*Biggs and Stokseth*, 1996]. *D. geminata* is considered to be well adapted to a wide range of hydraulic habitats in turbulent streams and has been observed to persist preferentially in stable channels and more regulated flow regimes such as downstream of lakes and reservoirs [*Kilroy et al.*, 2005; *Kirkwood et al.*, 2009]. Thus it has been suggested that the primary control on the removal of *D. geminata* mats is scouring as a result of sufficiently high flows to initiate physical disturbance of the substrate material [*Spaulding and Elwell*, 2007]. We hypothesize that the removal of *D. geminata* is therefore likely to be controlled primarily by a critical threshold of shear stress related to the potential for the disturbance of the substrate. This is shown in Figure 4 where the proposed disturbance removal function (R_d) is a function of increasing bed shear stress (τ) relative to a critical shear stress for disturbance of the substrate (τ_c). This critical shear stress value is usually defined in terms of a critical value for the non-dimensional Shields stress parameter (θ_c) [*Lorang and Hauer*, 2003], as shown in equation (1),

$$\tau_c = \theta_c(\rho_s - \rho_w)gD \tag{1}$$

where ρ_s and ρ_w are the density of sediment and the density of water respectively, g is the acceleration due to gravity and D is the median diameter of the substrate.

[17] The critical disturbance threshold for sediment transport in rivers is a function of both channel slope and bed
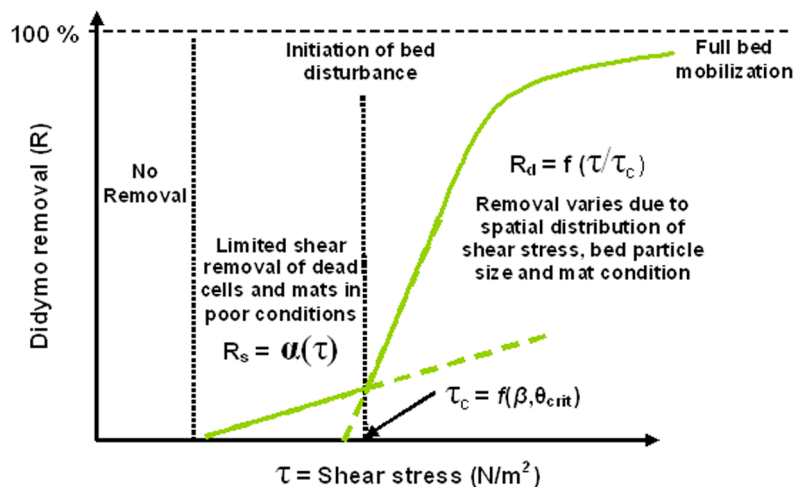
Figure 4. Proposed relationship between average bed shear stress and *D. geminata* removal (R) showing that the bulk of biomass removal (R_d) occurs above the critical value for bed disturbance (τ_c), but that below this value there is likely to be some shear removal (R_s), particularly of dead cells and mats in poor condition defined by the shear removal parameter (α). The critical value for bed disturbance is a function of the critical Shield's stress for the bed material (θ_{crit}) and a factor (β) accounting for the influence of the mats themselves.

particle size distribution [*Mueller et al.*, 2005]. Hence determining the critical flow requirements for bed disturbance and the removal of *D. geminata* requires site-specific information on channel morphology, substrate stability, the magnitude, timing and duration of high flow events. An additional complicating factor is the impact of the mats themselves on the near bed hydraulic conditions. *D. geminata* mats have been shown to reduce form-induced stresses and near-bed turbulent velocity fluctuations, which may reduce the risk of detachment [*Larned et al.*, 2011]. It is likely therefore that the flow rate necessary to produce the critical shear stress required for bed disturbance is higher in the presence of thick mats compared to either a bare streambed or where individual *D. geminata* colonies do not form a continuous mat on the streambed. This requires the consideration of an additional adjustment factor (β) for determining the critical removal threshold as shown in Figure 4. This factor is a function of both the mat morphology and the extent of coverage of the streambed. The magnitude of β is currently unknown but it is likely to be quite significant for thick mats that completely blanket the streambed.

[18] At flows less than the critical disturbance threshold, it is likely that there will still be some removal due to the increasing shear stress associated with detachment of cells, colonies, or entire mats from the underlying substrate. The removal of benthic algae by hydrodynamic forces can take many forms dependent on not only the intrinsic properties of the mat, but also the health of the mat and the level of pre-conditioning, i.e., the range of shear stresses to which the mat is typically exposed [*Biggs and Thomsen*, 1995]. The specific shear removal function for *D. geminata* (R_s) is currently unknown. As an initial estimate we proposed that R_S increasing linearly with shear stress above a critical value (Figure 4), but that the shear removal parameter (α) is likely to be low for healthy, well-conditioned mats. Not shown in

this graph are other potential random disturbances events such as physical detachment by the movement of fishermen and other recreational users or other natural disturbance events.

[19] A final consideration is that the removal of benthic algae is limited by the availability of removable material due to the history of previous events. Further, the biomass remaining after any flood should be expected to be relatively difficult to remove, either because it is intrinsically more resistant to shear or abrasion, or because it dwells within protected habitat (more stable substratum, low hydrodynamic shear, etc.). Two successive flood events are therefore unlikely to result in the same amount of removal unless there has been sufficient time between the flood events for the mats to recover. Rather, the impact of the second flood event is likely to be only as big as the difference in the magnitude of the flood events and the amount of biomass remaining after the removal due to the initial flood event. Hence it is important to not only consider the magnitude of the disturbance event, but also the duration of the event, the time-history of disturbance events, and the opportunity for regrowth between events. *Larned et al.* [2007], for example, found that the days since a flood event that produced significant bed disturbance was more significant than instantaneous hydraulic conditions, light availability, or water chemistry in determining the overall *D. geminata* abundance at a number of sites in New Zealand.

6.　Colonization and Recovery After Disturbance

[20] Flow rate is important in the colonization of benthic algae and recovery after a disturbance event because it impacts both the delivery rate of new cells and the near-bed surface hydraulics that control the ability of the new cells to attach to the substrate material [*McCormick and Stevenson*, 1991]. The potential for colonization of the substrate by
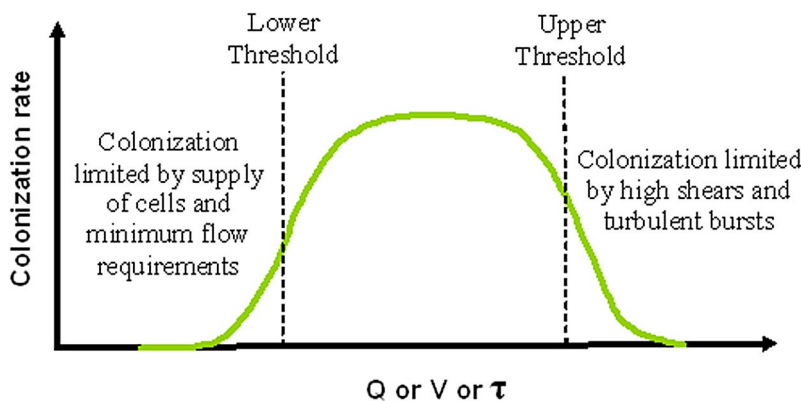
Figure 5. Proposed relationship between the colonization rate and increasing flow (Q), velocity (V), or shears stress (τ).

new cells can be considered to be a parabolic or Gaussian function of discharge or average velocity [*Saravia et al.*, 1998]. Alternatively it could be considered in terms of threshold values as shown in Figure 5. An upper threshold defined by a critical flow, velocity or shear stress would be related to the limit at which new cells can adhere to the substrate. This threshold value would be a function of the near-bed turbulence conditions, the roughness of the substrate, the presence of micro-refugia such as crevices, and the extent of the benthic algal mat—either newly grown or residual mats. The lower bound would be determined by the input of cells from upstream, as well as the minimum flow condition defining the habitat window for *D. geminata* growth.

[21] Currently neither of the upper or lower flow related threshold values are known for quantifying the potential for colonization of the substrate by *D. geminata.* It has been shown that colonization of *D. geminata* cells after a disturbance event is indeed influenced by the micro-topography of the substrate material [*Bergey et al.*, 2010] and the concentration of new cells arriving from upstream [*Flöder and Kilroy*, 2009]. The presence of residual *D. geminata* mats is therefore also likely to affect the colonization of new cells because of the impact of the mats on the near-bed hydraulic conditions [*Larned et al.*, 2011].

7. Distinguishing Mat Growth From Cell Division

[22] The importance of distinguishing between the growth of diatom cells and the growth of diatom mats has been shown even when considering a single limiting nutrient because different biophysical mechanisms control the growth of cells and the development of colonies [*Bothwell*, 1989]. In extensive *D. geminata* colonies or mats, the bulk of the biomass consists of stalk material [*Whitton et al.*, 2009]. As with most diatom species, cell division and growth requires energy in the form of light and key nutrients such as nitrogen, phosphorus and silica. The stalk material, however is primarily a polysaccharide [*Gretz*, 2008]. Therefore we hypothesize that stalk production is less dependent on nutrient availability than cell production because the carbohydrates making up the stalk material incorporate few nutrients.

[23] This hypothesis is supported by observations of the relationship between the frequency of dividing cells and the length of stalk material in controlled experiments that varied the available light and nutrient concentrations [*Kilroy and Bothwell*, 2011]. Under high light levels, low nutrients are associated with stalk elongation and higher nutrients are associated with greater cell division. In high light environments there is sufficient energy available for either stalk synthesis or cell reproduction. Under low nutrient conditions, however, cell production is nutrient limited and so the available energy goes into the production of stalk material leading to the thick mats seen under oligotrophic conditions.

[24] The proposed response of *D. geminata* to increasing nutrient concentrations is shown in Figure 6. At low stream water nutrient conditions, stalk production is high, but cell growth is low, as the available energy goes into stalk lengthening rather than cell division. Longer stalks help to position the cells further into the free stream in order to improve access to limited nutrients and light. Under nutrient-limiting conditions *D. geminata* is able to produce stalk biomass faster than competing benthic algal are able to produce biomass through cell division and growth. This gives *D. geminata* a competitive advantage, resulting in extensive proliferation in nuisance blooms. Under these conditions, it is also likely that there is a positive feedback with the mats aiding in the acquisition of dissolved phosphorus either through complex biogeochemical process within the mat [*Sundareshwar et al.*, 2011], the hydrolysis of trapped particulate sources [*Ellwood and Whitton*, 2007], and/or impacts on the nearbed hydrodynamics that increase turbulent mixing and nutrient cycling between the stream water and the mats [*Larned et al.*, 2011].

[25] As stream water nutrient conditions continue to increase, more of the available energy for growth goes into cell division as opposed to stalk production. The total biomass produced either remains constant with only a change in the mix between mat biomass and cell biomass, or potentially declines due to the greater energy requirements for cell production. At the same time, competing benthic algae also become less nutrient limited and have increased growth rates. At some critical threshold of nutrient concentration, *D. geminata* loses its competitive advantage and can be
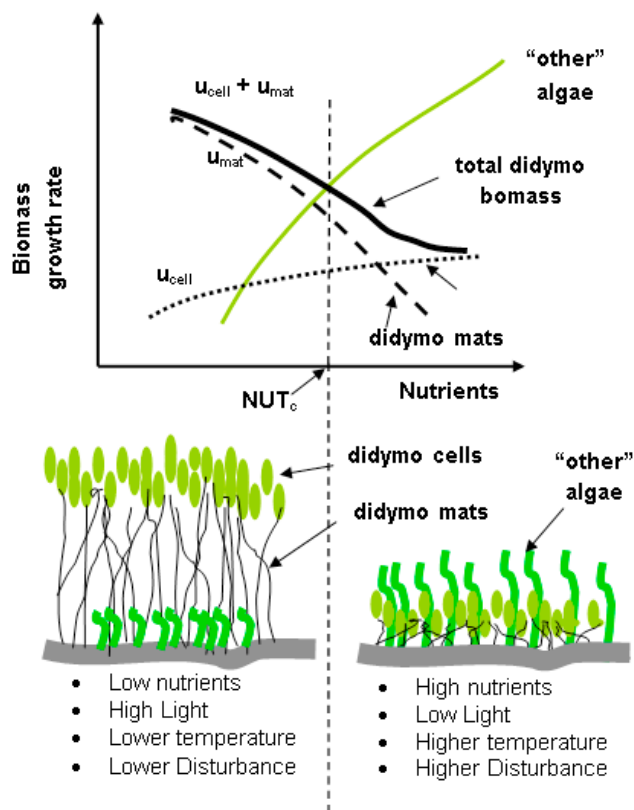
Figure 6. Hypothesized relationship between biomass growth rate (ΔB/Δt) and nutrient concentrations for cells, mats, and total biomass of *D. geminata* compared to other potentially competing benthic algae. The critical nutrient threshold (NUT$_c$), indicated by the dashed line, is the point at which *D. geminata* loses its dominance over competing algae.

overgrown on the streambed and the potential for nuisance blooms is reduced. What this threshold is, or even which are the defining variables, is currently unknown.

8. A Preference for High Light Environments

[26] For *D. geminata* light and carbon are the key building blocks required for the production of stalk material. Higher light availability has been shown to have a positive impact on the cell division rate [*Bothwell and Kilroy*, 2011] and stalk length [*Kilroy and Bothwell*, 2011] of *D. geminata*, but it has not yet been determined if light availability significantly influences spatial and temporal patterns of *D. geminata* abundance and mat thickness. The critical light availability threshold for the formation of nuisance blooms is therefore currently unknown and is indicated in the proposed habitat window for *D. geminata* (Figure 3) by a threshold value of photosynthetically active radiation (PAR) reaching the streambed (PAR > PAR$_c$).

[27] Part of the challenge with evaluating the role of light in the growth dynamics of benthic algae is accurately determining the amount of light reaching the cells on the streambed. The amount of light reaching the streambed varies significantly in both space and time, and is a function of many variables including latitude, elevation, topography,

channel aspect, channel slope, canopy shading, water depth, dissolved organic carbon (DOC), total suspended solids (TSS), and the presence of phytoplankton in the water column [*Davies-Colley*, 1990]. These variables are functions not only of the location and geometry of the stream reach, but also of variations in flow and suspended particle concentration [*Julian et al.*, 2008]. Failure to consider these site-specific and flow-specific controls on the penetration of light to the streambed may explain why previous studies looking at the seasonal dynamics of *D. geminata* growth were unable to identify a significant positive relationship between the seasonal variation in light and *D. geminata* growth [*Larned et al.*, 2006].

9. Temperature as a Controlling Variable

[28] Although *D. geminata* cells have been observed in a wide range of average stream temperatures [*Spaulding and Elwell*, 2007], temperature is still thought to be important in defining the habitat window for *D. geminata*. In particular, *Kumar et al.* [2009] showed that cooler temperatures in the warmest quarter of the year were positively correlated with the presence of *D. geminata*. Lower stream water temperatures are potentially important in the production of stalk material and the hydrolysis of organic phosphorus by the enzymes on the stalks [*Whitton et al.*, 2009]. Lower temperatures could also promote the uptake of other limiting nutrients such as nitrogen, as has been shown for marine diatoms in cool regions of the ocean [*Lomas and Gilbert*, 1999]. Alternatively *D. geminata* could simply be well adapted to living in cold temperatures as defined by its traditional habitat and has not (as yet) adapted to warmer stream conditions, or is dominated by other forms of benthic algae that have faster growth rates in warmer waters. It may also be possible that temperature is not important, but simply that streams meeting the other requirements that give *D. geminata* its competitive advantage, i.e., low nutrients and high light availability, tend to also be cooler due to their locations at higher elevations or higher latitudes.

[29] Until the apparent preference for colder temperatures is explained, the significance of temperature on defining the habitat window for *D. geminata* is shown in Figure 3 as a threshold value of $T < T_c$. It is however unclear exactly what measure of stream water temperature is significant, what the critical values is, or even whether temperature is a primary control on *D. geminata* growth or just an indicator of other unknown controls.

10. Water Chemistry and Secondary Nutrients

[30] Low nutrient concentrations are typically thought to be the primary chemical control on the habitat window for *D. geminata*. Recent studies, however, have shown that a number of other chemical variables may play an important role in the growth of *D. geminata*. Iron and dissolved organic carbon (DOC) are considered to be important in the complex biogeochemical processes occurring within the mats that support the release of soluble reactive phosphorus from trapped particulate phosphorus [*Sundareshwar et al.*, 2011]. Observations in California show that increasing calcium concentration in stream water was also positively correlated to the presence of *D. geminata* [*Rost et al.*, 2011]. This is

attributed to the potential requirements for calcium as a component of the stalk material [*Gretz*, 2008].

11. Impacts of Grazing

[31] A discussion of the likely controls on the growth of any benthic algae would be incomplete without consideration of grazing pressure as a top-down control [*Allan and Castillo*, 2007]. The impact of grazing on *D. geminata* is still unknown, but it is thought to be insignificant because the mats are primarily composed of large amounts of generally unpalatable stalk material [*Spaulding and Elwell*, 2007]. Other studies on the interaction between benthic algae and macro invertebrates in mountain streams concluded that grazing was not a significant control as the highest abundance of macroinvertebrates coincided with the greatest concentration of algal biomass [*Lewis and McCutchan*, 2010]. *Biggs et al.* [1999] also concluded that in many cases invertebrate grazing does not limit the growth of periphyton since it is generally well adapted to a certain level of grazing pressure. This does not mean that grazing can be completely ignored as a potential control, but that grazing effects are likely to be dominated by other factors such as variability in flow, light availability and water chemistry. Understanding the interaction between *D. geminata* and macroinvertebrate communities is therefore still an important area for future research particularly in establishing the impact that nuisance blooms have on habitat structure and the functioning of stream ecosystems [*Gillis and Chalifour*, 2010; *Kilroy et al.*, 2009].

12. Summary of the Conceptual Model

[32] In this paper we have attempted to synthesize existing knowledge about the stalk forming diatom *D. geminata* in order to make proposals about the critical aspects controlling the blooming behavior and persistence of this nuisance diatom. The key proposals contained within the conceptual model are summarized here. These proposals are premised on our interpretation of the existing knowledge and are intended to aid in the development of future research agendas and ultimately the modeling of growth dynamics that can be of use to water resource managers in areas threatened by future nuisance blooms. The key proposals of the conceptual model are as follows:

[33] 1. Translocation by humans is a significant vector for the invasion into new watersheds.

[34] 2. The spatial and temporal distribution of nuisance blooms can potentially be described by identifying critical threshold values for water chemistry, water temperature, nutrient concentrations, light availability and critical hydraulic parameters determined by the variability of flow and site specific geomorphological conditions.

[35] 3. Flood events sufficiently large to mobilize the substrate are the primary control on the removal of *D. geminata.*

[36] 4. Dense and thick mats alter local hydrodynamic conditions to favor persistence.

[37] 5. Determining the critical thresholds for the removal of *D. geminata* mats requires site-specific hydrological and geomorphological information, as well as better understanding of feedbacks between mat growth and hydrodynamic conditions.

[38] 6. Key to understanding the didymo paradox of high biomass production under low nutrient conditions is a separation of mat growth from cell growth.

[39] 7. The production of longer stalks under lower nutrient conditions, but high light availability is primarily as a result of photosynthetic overproduction.

[40] 8. Thicker mats resulting from this photosynthetic overproduction likely increase nutrient delivery from the free stream and potentially facilitate complex biogeochemical processes and nutrient retention within the mats setting up a positive feedback mechanism for enhanced growth and blooming behavior.

[41] 9. Light availability is important for the development of nuisance blooms and should be investigated further. Careful attention needs to be paid to how the availability of light is measured and how it is impacted by climate, channel geometry, flow rate and turbidity.

[42] 10. Stream temperature appears to be important in the preferred habitat for *D. geminata*, but it remains to be seen whether the organism has a competitive advantage at lower temperature relative to other benthic autotrophs or whether it is simply a case that areas favorable in terms of other constraints such as high light availability and lower nutrients concentrations are also generally colder resulting in a spurious correlation with temperature and *D. geminata* persistence.

[43] The development of a conceptual model helps us to identify the key drivers controlling the growth of *D. geminata* and to frame specific questions for further investigation. It is also the first step in developing a mechanistic model that can be used to test specific hypotheses on the observed complex spatial patterns and temporal dynamics seen in natural systems. The key parameters of the conceptual model are summarized in Table 1. While these parameters have been developed in the context of the didymo paradox, they also can be used to improve our understanding of the complex dynamics of stream ecosystems. The potential range of some of these parameters is suggested in Table 1, although the majority is currently unknown.

13. Future Research

[44] Suggestions for research to further develop and determine the key parameters in the proposed conceptual model are given in Table 1. We propose focusing on (1) defining the habitat window for both the survival and tendency to bloom of *D. geminata*, (2) determining the factors that control growth rates for cell division and mat development, and (3) determining the critical flow requirements for mat removal and recolonization after disturbance events. These research agendas require interdisciplinary understanding and a synthesis of data from a range of research disciplines including ecology, biogeochemistry, geomorphology and hydrology.

[45] Observations of *D. geminata* abundance must include co-located time series data on flow, temperature, light, water-quality and sediment dynamics. The main suggestions for future research therefore are (1) focused field data collection that includes both good spatial coverage and time series observations; (2) manipulation studies directly in streams or in streamside mesocosms to determined habitat windows and thresholds related to both survival and the potential to form nuisance blooms; and (3) laboratory flume experiments to establish removal and colonization thresholds.

Table 1. Suggested Components Defining the Proposed Conceptual Model for *Didymosphenia geminata* Ecology Dynamics and Related Parameters for Quantification

Model Component	Parameter	Description	Potential Range	Significant Controls
Defining the habitat window (Figure 3)	PAR_c	light requirement to support mat production and nuisance blooms	unknown but considered high	seasonal dynamics, shading, water depth, and water quality (e.g., TSS, clarity, and chl *a*)
	WQ_c	water chemistry limits for nuisance blooms	unknown	geology, groundwater interactions, and catchment characteristics
	T_c	temperature threshold for nuisance blooms	unknown but considered low	latitude, elevation, catchment characteristics, but may just be correlated to other controls
	Nut_c	nutrient threshold(s) for nuisance blooms	TDN < 2 mg/L[a], TDP < 1 μg/L[a]	catchment characteristics and human impacts
Defining the removal thresholds (Figure 4)	α	shear removal function (biomass/N)	unknown, but considered low	function of mat condition and suspended sediment load
	β	factor accounting for impact of *D. geminata* mats on the potential for bed disturbance	unknown, but significant for extensive mats[b]	function of mat thickness and extent of coverage
	θ_{crit}	critical shield's stress defining potential for bed disturbance	ranges between 0.03 and 0.07[c]	depends on site and substrate characteristics
Defining the growth rates (Figure 5)	u_{mat}	mat thickness growth rate (mm/d)	unknown but considered high	likely function of nutrient concentration (−), light (+), and carbon availability (+)
	u_{cells}	cell division rate (cells/d)	unknown	likely function of light (+), nutrient availability (+), and possibly mat thickness (+)
	K_{max}	maximum potential didymo biomass	unknown	light, nutrients, and space; may never be realized in dynamic stream system
Defining the colonization threshold (Figure 6)	$\tau_{cs}/Q_{cs}/V_{cs}$	thresholds for colonization potential	unknown	flow rate, substrate composition and roughness, and residual biomass

Model Component	Parameter	Research Suggestions	Management Potential
Defining the habitat window (Figure 3)		field observations and manipulations studies	identify threatened streams
		field observations and manipulations studies	identify threatened streams
		field observations and manipulations studies	identify threatened streams
		field observations and manipulations studies	identify threatened streams
Defining the removal thresholds (Figure 4)		field observations and flume experiments	increase sediment supply and use flushing flows
		field observations and flume experiments	use flushing flows large enough to mobilize bed material
		field observations and comparison with unimpacted streams	use flushing flows large enough to mobilize bed material
Defining the growth rates (Figure 5)		field observations and manipulations studies	increase nutrient supply to rivers
		field observations and manipulations studies	efficient timing for chemical dosing
		field observations and manipulations studies	both of the above plus identify threatened streams
Defining the colonization threshold (Figure 6)		field observations and flume experiments	maintain higher base flows after removal events

[a]Suggested range based on frequency of *D. geminata* abundance in the United States [*Spaulding and Elwell*, 2007].
[b]Studies show significant impact of *D. geminata* mats on near-bed hydrodynamics [*Larned et al.*, 2011].
[c]Based on a range of empirical studies of cobble and gravel bed rivers [*Buffington and Montgomery*, 1997].

[46] A final area for future research that is informed by the conceptual model is potential mitigation measures. One that requires further investigation and can potentially be implemented in a short timeframe and on a trial basis with minimal long-term impacts on the broader ecology is the use of managed flood releases or flushing flows from reservoirs upstream of impacted areas. There is growing awareness of the benefits of including flushing flows into the operating rules for reservoirs [*Kondolf and Wilcock*, 1996] including for the management of nuisance algal blooms [*Flinders and Hart*, 2009]. Flushing flows have been proposed as a potential mitigation measure for *D. geminata* in regulated reaches downstream of dams [*Kirkwood et al.*, 2009] and are currently being used on the Waiau River in New Zealand [*Kilroy*, 2010]. Developing a better understanding of the critical requirements for the removal of *D. geminata* as proposed in this conceptual model will help to quantify the effects of flushing flows and to determine more specifically the magnitude, duration and timing of flood events required for long-term control of *D. geminata.* This is essential information for water resources managers who have to balance the trade-off of many competing demands for water as a valuable and often scarce resource.

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