Université du Québec
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ÉTUDE DES FACTEURS CONTRÔLANT LA PRÉSENCE DE L'ALGUE *DIDYMOSPHENIA GEMINATA* ET DES IMPACTS DE SA PRÉSENCE SUR LE SAUMON ATLANTIQUE JUVÉNILE

Par

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RÉSUMÉ

L'algue *Didymosphenia geminata* est une diatomée à potentiel envahissant. Cette algue microscopique, attachée au substrat, peut sécréter des quantités phénoménales de mucilage et créer de vaste amas fibreux tapissant le lit d'une rivière. Autrefois considérée très rare et représentative d'une qualité d'eau impeccable, elle est maintenant répertoriée omniprésente dans les rivières oligotrophes à travers le monde. Au cours des deux dernières décennies, son émergence a créé un intérêt marqué de la part des écologistes et gestionnaires de rivières puisque sa biologie et les facteurs régissant son occurrence et sa sévérité sont méconnus. Au Québec, c'est à l'été 2006 que les premières proliférations massives de l'algue didymo ont été observées dans la rivière Matapédia. Le manque de connaissances à son égard, plus précisément sur sa distribution, les causes de l'apparition des proliférations et de l'impact négatif possible de cet envahissement sur le réseau trophique mais surtout sur le cycle de vie du saumon atlantique en rivière a créé un état de panique chez les gestionnaires et les utilisateurs des rivières à saumon. Il existait dès lors un urgent besoin de combler ces lacunes.

Afin de mieux comprendre les facteurs régissant tant la croissance cellulaire que la croissance des amas mucilagineux, un modèle conceptuel a été élaboré grâce à la collaboration de plusieurs chercheurs travaillant au Colorado, à l'île de Vancouver, en Nouvelle-Zélande et au Québec afin de colliger les observations et les données de terrain. Ce travail de synthèse a permis d'identifier les facteurs favorisant sa colonisation, sa croissance et sa persistance en rivière. La dynamique spatio-temporelle de l'algue didymo est dépendante de divers facteurs (ou conditions environnementales) dont les seuils critiques déterminent son comportement de prolifération. En rivière, la croissance d'algues benthiques est principalement déterminée par les variations saisonnières du débit, la température, la lumière et la chimie de l'eau. Ainsi, la connaissance des paramètres d'habitats favorables permet de déterminer si un bassin versant est favorable à la présence cellulaire de l'algue didymo et à la probabilité que celle-ci puisse y proliférer. Le modèle conceptuel permet d'établir la variabilité et la sévérité saisonnière du comportement envahissant de l'algue didymo en rivière.

Afin d'appliquer le modèle conceptuel développé à l'échelle du bassin versant, nous avons mis sur pied un réseau de suivi volontaire des proliférations d'algue didymo dans le bassin versant de la rivière Restigouche. Vingt-deux organisations différentes totalisant 70 bénévoles ont été formés à identifier et quantifier les proliférations d'algue didymo. Entre 2010 et 2015, 1 228 observations ont été réalisées. L'analyse de cette base de données, nous a permis de déterminer que 71% de la variabilité de la sévérité des proliférations durant l'été est inversement proportionnelle à l'intensité de la crue printanière. À l'échelle du tronçon, l'analyse des proliférations pour différents types de faciès-substrat a permis de d'identifier une préférence accrue pour les seuils.

Par la suite, afin d'appliquer le modèle conceptuel à l'échelle régionale, nous avons comparé la distribution de l'algue didymo dans trois régions de l'est du Québec (i.e. Gaspésie, Bas-St-Laurent et Côte-Nord) avec divers paramètres physico-chimiques de vingt-neuf rivières à saumon. Le

principal facteur régissant la présence-absence de cellules est le pH. Les diatomées ont des optimums de pH très spécifiques et la géologie contrastante de la Côte-Nord (Bouclier canadien) par rapport aux basses terres du Saint-Laurent et les Appalaches en Gaspésie, a permis d'identifier que les eaux acides riches en tanins et lignines ne sont pas favorables à la survie et la croissance de l'algue didymo.

Grâce à une meilleure connaissance des facteurs de contrôle de l'algue didymo à diverses échelles spatiales, nous pouvons déterminer les rivières à risque de proliférations massives. Au sein des rivières exhibant des proliférations, nous avons déterminé que les préférences d'habitat de l'algue didymo sont identiques à celles du saumon atlantique juvénile (i.e. eaux rapides, peu profondes, claires, froides, faible en nutriments avec un substrat grossier). Afin de déterminer l'ampleur de l'impact de la présence des proliférations sur le réseau trophique, nous avons vérifié son impact sur la communauté algale. La structure dense et fibreuse crée un environnement physique dans lequel plusieurs diatomées peuvent s'y loger. Nos résultats confirment que l'algue crée un habitat de choix pour les plus petites diatomées favorisant ainsi une plus grande diversité taxonomique. Malgré une augmentation de la complexité du biofilm suivant son épaississement, il n'y a pas d'impact supplémentaire sur la structure et la diversité taxonomique des échantillons.

Puisque la structure de l'habitat est modifiée par les tapis et que ces derniers sont susceptibles d'altérer la structure et le fonctionnement de l'écosystème, nous avons évalué l'effet des proliférations sur le comportement alimentaire des saumons juvéniles. Grâce à l'observation en apnée du comportement, nous pouvons conclure que les saumons juvéniles effectuent une plus grande proportion de quêtes benthiques en fonction du pourcentage de recouvrement algal. Ce changement de comportement n'est pas attribuable à une diminution des proies disponibles au sein de la dérive. Notre étude confirme la grande plasticité comportementale des saumons juvéniles face aux modifications de l'habitat.

Afin de vérifier l'impact des proliférations sur les ressources alimentaires et la diète des saumons juvéniles, nous avons utilisé l'approche par analyse d'isotopes stables. Cette approche permet d'établir un portrait intégré de l'utilisation des ressources par les poissons. Les signatures isotopiques divergentes entre les différents tissus des saumons confirment une modification de la diète saisonnière. Les saumons juvéniles en présence de l'algue didymo ont une diète moins diversifiée et appauvrie en carbone principalement composée de petits chironomides et de trichoptères. Malgré que l'indice de condition physique des saumons juvéniles soit similaire entre les deux sites, leur taille est plus petite dans le site avec proliférations. Les travaux futurs devront tenter de valider l'impact de la diminution de la qualité de la diète par les proliférations d'algue didymo sur le contenu en lipides des juvéniles.

Suite aux diverses collaborations internationales et discussions avec les gestionnaires, nous nous sommes rendus à l'évidence qu'il devait y avoir une recommandation sur les mesures de gestion vis-à-vis cette espèce. En fonction des connaissances scientifiques développées au fil des ans et plusieurs cas de gestion dans divers pays, nous avons recommandé aux gestionnaires d'éduquer les utilisateurs à vérifier, nettoyer, sécher et congeler leurs équipements. Que l'algue didymo soit une espèce exotique ou indigène, elle peut être propagée. De plus, la mise en valeur des saines pratiques permettent de limiter la propagation d'autres organismes pouvant potentiellement être plus dévastateurs que l'algue didymo.

Les résultats de cette thèse contribuent à l'avancement des connaissances sur les facteurs de contrôle de l'algue didymo tant à l'échelle microscopique que macroscopique. En plus d'avoir contribué à élaborer le modèle conceptuel, nous l'avons amélioré en l'appliquant à diverses échelles spatiales : à l'échelle du tronçon et du bassin versant ainsi qu'à l'échelle régionale. C'est d'ailleurs la première étude à élaborer un réseau de suivi des proliférations par l'implication des acteurs du milieu ainsi qu'une des seules études à avoir examiné la variabilité interannuelle sur une période de six ans. C'est également la première étude à avoir évalué l'impact de l'algue didymo sur les communautés périphytiques dans l'est du Canada. De surcroît, c'est la première étude exhaustive qui a évalué l'effet des proliférations sur l'écologie du saumon atlantique juvénile. Les recherches menées sur le comportement alimentaire est également novateur et contribue considérablement à la compréhension des mécanismes et les interactions entre les divers niveaux trophiques et l'impact sur les salmonidés.

ABSTRACT

Didymosphenia geminata is mat-forming nuisance diatom. This epilithic microscopic alga can secrete copious amounts of mucilage creating thick and extensive mats covering the entire riverbed. Once considered very rare and representative of pristine water quality, it is now ubiquitous in rivers around the world. Over the past two decades, this alga has emerged as a nuisance diatom and generated much interest among freshwater ecologists and river managers alike. Nonetheless, controlling factors governing the occurrence and severity of *D. geminata* are still not well understood. In Quebec, the first massive proliferations of *D. geminata* were reported in 2006 in the Matapedia River. There was an urgency to fill this knowledge gap as managers and government agencies panicked at the lack of knowledge regarding its distribution, the causes of its onset and mostly, fear of that this alga would act as an additional stressor to Atlantic salmon populations.

To better understand controlling factors of both cell division and mat formation, a conceptual model was developed with the collaboration of several researchers working in Colorado, Vancouver Island, New Zealand and Quebec to collate observations and field data. This synthesis work helped identify the factors favoring its colonization, growth and persistence in rivers. The spatiotemporal dynamics of *D. geminata* are dependent on various dynamic thresholds of flow, temperature, light and water chemistry within the habitat window. We can therefore test various arrays of these parameters to determine whether rivers are likely to present occasional to persistent *D. geminata* mats.

To test and improve upon the conceptual model at various spatial scales, we developed a monitoring network for *D. geminata* mat presence. Twenty-two different organizations totaling 70 volunteers were trained to identify and quantify the proliferations of *D. geminata*. Between 2010 and 2015, 1 228 observations were made. The analysis of this database helped determine that 71% of the variability of *D. geminata* severity is inversely proportional to the intensity of the spring flood. At the reach scale, habitat type was determinant for presence-absence of mats with a strong significant preference for riffles.

At the provincial scale, we compared the distribution of *D. geminata* in three regions of eastern Quebec (i.e. Gaspesie, Bas-St-Laurent and Cote-Nord) against numerous water chemistry parameters for twenty-nine rivers. At the broad regional scale, pH was the most important factor governing the presence-absence of cells. Diatoms have very specific pH optima and the contrasting geologies between regions confirmed that low pH and high tannins and lignin are not favorable to the survival and growth of *D. geminata*.

Habitat preferences for *D. geminata* mats are identical to those of juvenile Atlantic salmon (i.e. shallow, fast, clear, cool, low nutrient and coarse substrate). To determine the extent of the impact of the presence of mats on the food web, we verified its impact on the algal community. The dense interwoven matrix creates a suitable physical environment for small diatoms, thus promoting greater taxonomic diversity. Despite an increase in the complexity of the biofilm with mat accrual, there is no additional impact on the structure and taxonomic diversity of the samples.

D. geminata effects to higher trophic levels have been suspected since the structure of the habitat is modified and could alter the structure and functioning of the ecosystem. We studied the foraging behaviour of juvenile Atlantic salmon in contrasting *D. geminata* severities. With increasing percent cover of the alga, juvenile Atlantic salmon switch from a drift-foray to benthic-foray strategy. This change in behavior is not due to limited drifting prey availability. Our results reinforce the notion that juvenile Atlantic salmon have high behavioral plasticity in response to habitat changes.

To test the impact of mats on juvenile salmon diet, we used a stable isotope analysis approach. This approach provides an integrated view of resource use by fish. Contrasting isotopic signatures between the liver and muscle tissues confirm a change in the seasonal diet. Juvenile salmon sampled in the *D. geminata* impacted site have a less diversified and carbon-depleted diet composed mainly of small chironomids and Trichoptera. Juvenile salmon condition factors and C:N ratios were not different between sites, though their size is smaller in the impacted site. Future work should focus on the effects of reduced prey quality on lipid content of fish.

Over various international collaborations and discussions with managers, it became clear that there was a need for a clear and standardized recommendation on management measures for this nuisance species. Based on recent scientific knowledge and several management cases in various countries, we recommended that managers educate users to check, clean, dry and freeze their equipment. Regardless of whether *D. geminata* is an exotic or native species, it can be spread. In addition, the development of best practices limits the spread of aquatic organisms as others may be far more devastating than *D. geminata*.

The results of this thesis contribute to the advancement of knowledge on the controlling factors of *D. geminata* for both cells and mats. In addition to contributing to the development of the conceptual model, we have tested and improved it by applying it to a variety of spatial scales: at the reach, watershed and regional scales. This is the first study to develop a monitoring network for mat severity with the involvement of local stakeholders. It is also the first study to evaluate the impact of *D. geminata* on periphytic communities in eastern Canada. Moreover, it is the first comprehensive study that has evaluated the effect *D. geminata* mats on juvenile Atlantic salmon ecology. Research on foraging behavior is also innovative and contributes significantly to the understanding of the mechanisms and interactions by which *D. geminata* impacts various trophic levels and salmonids.

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SYNTHÈSE

CHAPITRE 1
INTRODUCTION

1.1 L'algue didymo et son émergence dans les rivières à saumon de la Gaspésie

En juillet 2006, des amas d'algues massifs et laineux ont été recensés sur plus de 35 km du lit de la rivière Matapédia, une rivière à saumon de renommée internationale située dans la région gaspésienne de la province de Québec (Canada). L'algue était si abondante que les activités de pêche sportive ont été entravées pendant plusieurs jours par les dépôts d'algues qui s'enroulaient autour de la soie des pêcheurs à la mouche. Il s'est avéré que l'importante biomasse était le produit des proliférations de *Didymosphenia geminata* (Lyngbye) M. Schmidt, une diatomée à fort potentiel envahissant communément appelé « algue didymo ».

Figure 1.1 Tapis massifs de *D. geminata* recouvrant le lit de la rivière Duval, tributaire de la rivière Bonaventure en Gaspésie, à l'été 2013. Source : Michel Chouinard.

Puisque cet événement constituait la première observation de proliférations massives au Québec, cela a provoqué un véritable vent de panique chez les gestionnaires et utilisateurs de rivières gaspésiennes. Ces derniers craignaient les impacts négatifs potentiels de l'algue didymo sur la ressource salmonicole sur laquelle repose l'économie locale (Whoriskey, 2008). La présence des proliférations modifiant la base du réseau trophique, ces dernières sont susceptibles d'altérer la structure et le fonctionnement de l'écosystème (Larned *et al.*, 2007. Gillis & Chalifour, 2010) et, il est en conséquence justifié d'appréhender un effet possible sur les populations de poissons lotiques comme celles du saumon atlantique. Malheureusement, très peu de connaissances scientifiques sont disponibles sur le sujet et il existe un besoin urgent de combler cette lacune.

De fait, la biologie même de l'algue didymo est encore extrêmement mal connue. Outre les quelques observations disponibles qui indiquent que *D. geminata* préfère les eaux faibles en nutriments, où le substrat est stable, la turbidité est faible et le pH est neutre (Kirkwood *et al.*, 2007; Spaulding & Elwell, 2007), peu d'informations quantitatives existent concernant les facteurs physico-chimiques qui régissent l'occurrence, l'ampleur et la persistance des proliférations de didymo. Depuis 2006, la progression de didymo s'est étendue rapidement à plusieurs rivières de la Gaspésie, du Nouveau-Brunswick ainsi qu'à la quasi-totalité des états du nord-est des États-Unis. En Nouvelle-Zélande, elle est maintenant considérée « menace nuisible et indésirable » (Vieglais, 2008) et constitue, selon Blanco et Ector (2009), la plus grande menace à la pérennité des milieux lotiques à l'échelle internationale.

1.2 Objectifs de recherche

En raison de l'émergence récente de l'algue didymo et du manque de connaissances concernant sa biologie et ses impacts sur l'écosystème, il existe actuellement un besoin urgent de (1) comprendre les conditions physico-chimiques contrôlant la présence, l'occurrence et l'ampleur de ses proliférations, et (2) déterminer l'effet de cette algue sur le saumon atlantique. Ces deux questions constituent les principaux objectifs de recherche de ce projet de doctorat.

Dans le cadre du premier volet de la thèse, le premier objectif spécifique consiste à élaborer un modèle conceptuel décrivant la dynamique des facteurs pouvant jouer un rôle dans la colonisation, la croissance et la persistance des proliférations de *D. geminata.* Le deuxième objectif spécifique vise à développer un réseau de surveillance permettant le suivi de la distribution et de la sévérité des proliférations. Ainsi, par l'engagement des acteurs locaux, une base de données pouvant être utilisée dans le but de tester le modèle conceptuel à diverses échelles spatiales sera créée.

Le deuxième volet de la thèse vise à évaluer l'impact de la présence des proliférations sur le réseau trophique. Afin d'identifier les mécanismes par lequel l'algue didymo altère la structure et les fonctions écologiques du réseau trophique en rivière, le premier objectif spécifique consiste à analyser l'impact des proliférations sur les communautés algales. Par la suite, le deuxième objectif spécifique évalue l'impact de la sévérité des proliférations sur la disponibilité des proies et le comportement alimentaire du saumon atlantique juvénile en rivière. Le troisième objectif spécifique consiste à décrire l'impact de la présence des proliférations sur la qualité des proies et la diète du saumon atlantique juvénile.

1.3 Subdivision de la thèse

Cette thèse comprend 11 chapitres et est structurée en deux volets visant à approfondir tant les connaissances concernant l'écologie de *D. geminata* que ses effets sur l'écologie du saumon juvénile. L'introduction (chapitre 1) présente la problématique de l'algue didymo dans l'est du Canada. Par la suite, une revue de littérature exhaustive (chapitre 2) aborde la distribution, la biologie et les impacts potentiels de l'algue didymo et fait l'état des connaissances à ce jour. Le troisième chapitre constitue un résumé détaillé des travaux réalisés dans le cadre de ces deux axes de recherche sous forme de courts résumés pour chacun des articles présentés dans les chapitres suivants. Le chapitre 3 se veut une synthèse substantielle et intégrée du travail réalisé au sein des deux axes de recherche. Le chapitre 4 présente les contributions scientifiques réalisées parallèlement aux travaux de la thèse de doctorat ainsi que les perspectives d'avenir en ce qui concerne la recherche sur l'algue didymo. Le premier volet, est constitué des chapitres 5 à 7 inclusivement. Le chapitre 5 présente un article concernant le modèle conceptuel de l'algue didymo publié dans le *Journal of Geophysical Research.* Les chapitres 6 et 7 présentent l'application et la validation de ce modèle conceptuel. Plus précisément, le chapitre 6 détaille la méthodologie réalisée pour l'élaboration d'un réseau de suivi des proliférations de l'algue didymo dans l'est du Canada. Ce chapitre incorpore les données recueillies dans le cadre de cet effort collaboratif afin d'identifier les facteurs hydrologiques et géomorphologiques qui régissent l'occurrence et la sévérité des proliférations à l'échelle du bassin versant. Le chapitre 7, quant à lui, présente l'état des facteurs physico-chimiques qui contrôlent la distribution et la biogéographie de l'algue didymo à l'échelle du Québec. Le deuxième axe de recherche portant sur les impacts des proliférations de l'algue didymo sur les diverses composantes du réseau trophique, est constitué des chapitres 8 à 10 inclusivement. Le chapitre 8 présente les travaux réalisés et publiés dans *Diatom Research* sur l'impact des proliférations sur la structure et la diversité de la communauté de diatomées en rivière. Le chapitre 9 fait état des conséquences de la présence des amas mucilagineux de didymo en rivière sur le comportement alimentaire du saumon atlantique juvénile. Le chapitre 10, quant à lui, présente les résultats d'analyses isotopiques de la présence de l'algue didymo sur le réseau trophique, notamment des impacts sur la qualité des proies disponibles et sur le saumon atlantique juvénile. Finalement, le chapitre 11, quant à lui, est un article publié dans *Diatom Research* qui détaille les obstacles associés à la gestion de l'algue didymo et émet des recommandations aux gestionnaires de rivières en considérant les avancées scientifiques sur l'algue didymo à l'échelle internationale.

CHAPITRE 2
REVUE DE LITTÉRATURE

Lorsque ce projet a été initié en 2008, les connaissances et les prémisses scientifiques étaient différentes de ce qu'elles sont devenues en 2017. La problématique, présente à l'échelle internationale, a généré une évolution rapide des connaissances au cours de la dernière décennie puisque plusieurs chercheurs à travers le monde étudient les diverses facettes de l'algue didymo.

2.1 Biologie de l'algue didymo

L'algue *Didymosphenia geminata* (Lyngbye) M. Schmidt est une diatomée unicellulaire à paroi siliceuse. La cellule, une frustule composée de deux valves symétriques, sécrète un tube de mucopolysaccharides par le pore apical (Figure 2.1). Par division végétative, les frustules se divisent et causent, par conséquent, la division des tubes. Lorsque les conditions sont favorables, *D. geminata* colonise ainsi le milieu par la multiplication des tubes (Spaulding & Elwell, 2007) qui continuent à bifurquer à chaque division créant ainsi une croissance exponentielle des amas (Kilroy, 2004).

Figure 2.1 Tubes et frustules de *D. geminata*. Les tubes sont sécrétés par le frustule. La division végétative est représentée par la présence de deux frustules sur un même pédoncule. Source : Robert Chabot.

Fixés au substrat des cours d'eau, ces amas ont l'apparence de « pompons » (Figure 2.2) (Kawecka & Sanecki, 2003), dont la structure arborescente permet de maintenir les cellules photosynthétiques en périphérie, maximisant ainsi leur exposition à la lumière et aux vitesses d'écoulement, et favorisent les apports d'éléments nutritifs nécessaires à la croissance de l'algue (Round *et al.*, 1990; Burkholder, 2009). En fait, selon Ellwood et Whitton (2007), la structure et la fonction des tubes peuvent favoriser la présence de proliférations dans des conditions pauvres en nutriments puisque les tubes témoignent d'une forte activité enzymatique pouvant hydrolyser le P-organique présent dans l'eau et le rendre disponible à *D. geminata.*

Figure 2.2 Amas de tubes de *D. geminata* en colonisation. Source : Jordane Clermont.

Lorsque la diatomée se retrouve en conditions optimales, sa croissance est rapide et l'on appelle alors cette expansion une prolifération. Les tubes, composant la majeure partie de la biomasse, forment alors un tapis recouvrant parfois entièrement le substrat sur plusieurs centimètres d'épaisseur (Figure 2.3) (Larned *et al.*, 2007). Ces tapis mucilagineux sont résistants à la dessiccation et à la biodégradation et peuvent demeurer fixés sur le lit de la rivière pendant quelques mois (Gretz *et al.*, 2007; Spaulding & Elwell, 2007).

À l'échelle mondiale, l'ampleur des proliférations de *D. geminata* témoignent d'un comportement d'espèce envahissante (James, 2011). Certains indices permettent de suggérer qu'une variante génétique de cette diatomée soit responsable de l'augmentation des proliférations massives à l'échelle planétaire (Kirkwood *et al.*, 2007). Pourtant, dans certains cas, elle peut se trouver en faible abondance sans conséquences indésirables (Kilroy & Bothwell, 2011).

Figure 2.3 Tapis fibreux de *D. geminata* tapissant le lit de la rivière Upsalquitch. Source : Andrew Olive

2.2 Facteurs physico-chimiques favorisant sa présence et sa prolifération

Plusieurs facteurs pouvant expliquer la répartition et l'ampleur des proliférations de l'algue didymo à l'échelle internationale ont été proposés par divers experts (Campbell, 2005; Spaulding & Elwell, 2007). Par le passé, les proliférations de *D. geminata* se produisaient surtout dans les eaux ayant de faibles concentrations en nutriments (Spaulding & Elwell, 2007; Kilroy & Bothwell, 2011). Un portrait des seuils de tolérance des facteurs physico-chimiques de *D. geminata* semble cependant démontrer que celle-ci se développe maintenant dans un plus large éventail de conditions qu'initialement décrite, ce qui a amené Spaulding et Elwell (2007) à la qualifier d'algue ubiquiste. Néanmoins, certains facteurs environnementaux semblent exercer un effet important sur la colonisation, la croissance et la persistance des tapis mucilagineux de *D. geminata*.

Ainsi, des études ont démontré que bon nombre de variables chimiques telles que le pH et la conductivité peuvent jouer un rôle important dans l'établissement et la croissance de *D. geminata* (Spaulding & Elwell, 2007; Rost *et al.*, 2011). Contrairement à la plupart des proliférations formées par d'autres espèces d'algues (Anderson *et al.*, 2002), *D. geminata* parvient à former une biomasse épaisse et étendue dans des conditions oligotrophes (Kirkwood *et al.*, 2007; Kilroy & Bothwell, 2011). Parmi les principales conditions environnementales qui affectent le développement des nattes, la faible disponibilité en phosphore (P) est sans doute la plus critique. Ces proliférations surviennent particulièrement lorsque la concentration en phosphore inorganique est limitée, soit lorsque les ratios N :P sont déséquilibrés, et que les niveaux d'intensité lumineuse sont élevés (Kilroy & Bothwell, 2011). Bothwell *et al.* (2014) ont noté que les tapis dans les cours d'eau néo-zélandais étaient habituellement limités à des concentrations moyennes annuelles de P réactives solubles inférieures à 2 µg L^{-1}. En outre, les augmentations à court terme de la disponibilité du P peuvent accroître considérablement le taux de division cellulaire (Bothwell & Kilroy, 2011) et une augmentation prolongée de la disponibilité du P peut réduire l'épaisseur du couvert algal (Lindstrom & Skulberg, 2008; Kilroy & Bothwell, 2012; James *et al.*, 2015).

La production massive de tubes en présence de grande intensité lumineuse serait possiblement le résultat d'une surproduction photosynthétique. De plus, James (2011) a démontré que la disponibilité de la lumière était le facteur de contrôle le plus important de la présence et de l'abondance de didymo. Plusieurs mécanismes ont été proposés pour expliquer la prolifération de l'algue didymo dans des conditions fortement limitées en nutriments. Ellwood et Whitton (2007) et Bray *et al.* (2016) suggèrent que l'enzyme phosphatase alcaline présente dans les amas mucilagineux permetrait d'acquérir efficacement le P organique de l'eau. Sundareshwar *et al.* (2011) ont proposé que les tapis recyclent le P en libérant des complexes P-fer liés à l'intérieur du tapis anoxique. Cependant, Bothwell *et al.* (2012) ont contesté ce mécanisme en constatant que de nombreux tapis se produisent dans les ruisseaux à faible concentration en fer. Bothwell *et al.* (2014) ont suggéré que les tiges sont sécrétées seulement lorsque les conditions de P sont extrêmement faibles afin que les cellules soient localisées hors de la couche limite de diffusion afin qu'elles puissent acquérir plus de P de la colonne d'eau. D'autre part, Kilroy et Larned (2016) ont testé l'importance de l'azote sur la biomasse mucilagineuse et ont rapporté que l'azote inorganique dissous peut stimuler la croissance du tapis lorsque le P et l'azote sont limitants.

La température de l'eau semble également influencer les périodes de croissance ainsi que l'ampleur de la biomasse produite par cette algue. En fait, Kumar *et al.* (2009) ont démontré que la présence de *D. geminata* était positivement corrélée avec une température plus fraîche de l'eau lors du trimestre le plus chaud de l'année. En fait, des températures plus basses favoriseraient la production de tubes et l'hydrolyse du phosphore organique (Whitton *et al.*, 2009).

Plusieurs travaux permettent de confirmer que cette algue benthique est bien adaptée à l'environnement lotique (Bergey *et al.*, 2010; Cullis, 2011; Larned *et al.*, 2011). En fait, la tige de *D. geminata* est très résistante aux perturbations hydrologiques (Spaulding & Elwell, 2007). La capacité de didymo à adhérer au substrat contribue à sa présence et sa persistance dans cet environnement dynamique (Whitton *et al.*, 2009). De plus, la stabilité du régime hydrologique et un faible débit moyen représentent des facteurs favorisant la prolifération de *D. geminata* (Kirkwood *et al.*, 2009; Kumar *et al.*, 2009; Bergey *et al.*, 2010). Toutefois, une crue suffisante pour mobiliser le substrat, entrainera l'érosion de la biomasse algale.

Ainsi, le régime hydrologique, la température et la luminosité peuvent définir la variabilité saisonnière des proliférations de *D. geminata*.

2.3 Évolution de l'aire de distribution et causes potentielles de son émergence

Les proliférations de didymo ne sont pas récentes puisque l'on rapportait déjà des proliférations dans l'hémisphère nord au 19^{e} siècle (Blanco & Ector, 2009). Depuis quelques décennies, *D. geminata* a élargi son aire de distribution, et ce, tant au sein de sa répartition dite historique (native) qu'ailleurs où sa présence semble être un phénomène récent (Lagerstedt, 2007; Spaulding & Elwell, 2007; Whitton *et al.*, 2009). Autrefois cantonnée aux eaux froides et oligotrophes de l'hémisphère nord (Patrick & Reimer, 1975), didymo prolifère maintenant dans des conditions environnementales très variées (Blanco & Ector, 2009). Sa distribution s'étend maintenant au-delà des milieux oligotrophes (Duncan *et al.*, 2005). Kawecka et Sanecki (2003) rapportent que *D. geminata* prolifère dans les rivières mésotrophes de Pologne. À la fin des années 1980, des proliférations problématiques avaient été signalées dans les rivières de l'île de Vancouver (Sherbot & Bothwell, 1993). Par la suite, des proliférations ont également été signalées en Islande (Jonsson *et al.*, 2008), Norvège (Lindstrom & Skulberg, 2008) et dans l'ouest des États-Unis (Erickson *et al.*, 2004; Kumar *et al.*, 2009). En 2004, la présence de *D. geminata* dans l'hémisphère sud a été confirmée pour la première fois en Nouvelle-Zélande (Kilroy, 2004) et plus récemment, en Patagonie, au Chili (Reid *et al.*, 2012). Sa présence dans ces pays a été tellement intensive qu'elles ont mis les autorités locales en alerte. Depuis l’apparition de ce fléau en Nouvelle-Zélande, l’algue didymo est perçue comme une espèce envahissante indésirable selon le Biosecurity Act 1993, par la communauté scientifique, les gestionnaires et les instances gouvernementales.

En 2006, des proliférations de *D. geminata* ont été observés pour la première fois sur la côte est nord-américaine, dans la rivière Matapédia (Bothwell & Spaulding, 2008). Depuis, plusieurs proliférations ont été signalées sur la quasi-totalité des états de l’est des États-Unis; Vermont, Connecticut, New York, Maine, Maryland, Pennsylvanie, New Hampshire, Tennessee, Kentucky, Virginie et Virginie-Occidentale (divers communiqués de presse). Ce taux de propagation géographique sans précédent semble être attribuable à des introductions anthropiques via l’équipement de pêche sportive contaminé (Campbell, 2005; Bothwell *et al.*, 2009; Beville *et al.*, 2012).

Sur la côte Est du Canada, des proliférations d'intensité variable se produisent dans une vingtaine de rivières de la Gaspésie et du nord du Nouveau-Brunswick. Au Québec, depuis 2006, la majorité des bassins versants avoisinants celui de la rivière Matapédia ont été touchés par les proliférations d’algue didymo. En fait, près de 75% des cours d’eau de la péninsule gaspésienne et du nord du Nouveau-Brunswick présentent des proliférations occasionnelles à ce jour. La distribution actuelle de l’algue didymo au Québec semble limitée aux rivières gaspésiennes et à la rivière à Mars au Saguenay. Malgré de fortes probabilités d’apports en cellules par les utilisateurs et des conditions oligotrophes des rivières, les autres rivières à saumon du Saguenay et de la Côte-Nord sont toutefois exemptes de proliférations. Il est possible que les rivières de la Côte-Nord présentent des particularités pouvant limiter la présence de *D. geminata* mais ces raisons restent encore à être déterminées.

Deux hypothèses, parfois considérée opposées, ont été proposées afin d’expliquer l'apparition progressive des proliférations de l’algue didymo au cours des deux dernières décennies. La première, se base sur la probabilité de propagation, puisque les frustules étant résistants à la dessiccation et invisibles à l’œil nu, ils peuvent être transportés par les multiples usagers des cours d’eau (Kilroy & Unwin, 2011). Il a été proposé par Flöder et Kilroy (2009) que l’achalandage et une forte concentration de cellules favorise la récurrence et la persistance des proliférations. En Nouvelle-Zélande, la propagation progressive mais rapide de *D. geminata* à de nombreuses rivières de l'île du Sud suggère la dispersion typique d’une espèce envahissante, et ce, via des vecteurs humains (Kilroy & Unwin, 2011). Des études en Nouvelle-Zélande ont démontré que la rétention de l’humidité au sein des semelles de feutre suffit pour maintenir les cellules de didymo viables pendant plusieurs semaines (Kilroy *et al.*, 2007). Ceci accroît donc son potentiel de survie et augmente, par conséquent, le risque de propagation de didymo à l’échelle mondiale (Lagerstedt, 2007). Le modèle de propagation de *D. geminata* en Nouvelle-Zélande et au Chili supporte cette idée et suggère qu'il peut s'agir d'une espèce introduite dans certaines régions (Kilroy & Unwin, 2011; Montecino *et al.*, 2016).

Plus récemment, une deuxième hypothèse a émergé intégrant l'approche des idées que l'évolution des conditions environnementales pouvant favoriser la prolifération alors que les cellules y étaient historiquement peu abondantes (Lavery *et al.*, 2014). Les cellules de *D. geminata* sont souvent trouvées dans des rivières qui ne connaissent pas de tapis benthiques épais (Kilroy & Unwin, 2011), ce qui suggère qu'il existe différentes conditions pour soutenir la survie cellulaire et le développement des proliférations (Cullis *et al.*, 2012). Par conséquent, l'apparition de tapis de *D. geminata* nécessite à la fois la présence de cellules viables et des conditions environnementales appropriées pour le développement de la tige et du mat (Kuhajek *et al.*, 2014). Ici, nous appelons cette hypothèse d'évolution des conditions chimiques en tant que moteur de la prolifération comme l'hypothèse du changement environnemental. Étant donné l'évidence croissante que les conditions environnementales définissent la variabilité saisonnière et géographique de la biomasse des matrices de *D. geminata*, l'invasion en tant que principale cause de nouvelles occurrences de tapis est de plus en plus remise en question (par exemple Taylor & Bothwell, 2014).

Les bases de données actuelles sur la présence-absence de *D. geminata* sont éparses et trop succinctes pour permettre une analyse exhaustive des facteurs qui contrôlent la répartition de cette algue envahissante à l'échelle planétaire. De plus, la méthode de quantification de l'ampleur des proliférations n'est pas standardisée, ce qui nuit à la comparaison des données entre les régions ainsi qu'à la création de séries chronologiques mettant en évidence la dynamique saisonnière des proliférations.

2.4 Impact de didymo sur les caractéristiques physico-chimiques de l'habitat lotique

Malgré le fait que les proliférations de *D. geminata* fassent l'objet d'un bon nombre d'études scientifiques, la majorité d'entre elles portent sur la détermination des facteurs pouvant influencer cette diatomée et non sur l'effet mesurable que ces proliférations massives peuvent avoir sur les caractéristiques physico-chimiques des habitats aquatiques. Kilroy (2006) a démontré que la présence des tapis de *D. geminata* augmente les valeurs journalières de pH de la rivière Mararoa en Nouvelle-Zélande. D'autre part, une étude récente s'est attardée à l'effet des tapis fibreux sur les caractéristiques hydrauliques (Larned *et al.*, 2011). Les tapis réduisent la turbulence en uniformisant l'écoulement de la colonne d'eau mais augmentent la turbulence à l'interface tapis-eau. L'augmentation des forces de friction au niveau de cette interface crée un écoulement lent et diffus au sein du tapis. Ainsi, les auteurs proposent que *D. geminata* modifie son environnement hydrodynamique afin d'optimiser l'absorption et la rétention de nutriments par advection tout en minimisant les risques d'érosion par la force de cisaillement de l'écoulement.

2.5 Impacts de l'algue didymo sur le réseau trophique

Les algues, producteurs primaires, sont essentielles à la chaîne trophique en milieux lotiques (Biggs, 2000). Lorsque la productivité primaire d'un réseau trophique est modifiée, une cascade d'effets « bottom-up » se répercutent sur les niveaux trophiques supérieurs tels que les producteurs secondaires (macroinvertébrés benthiques) et les consommateurs (la faune ichthyenne) (Biggs, 2000; Larned *et al.*, 2007; Whitton *et al.*, 2009). Ainsi, l'importante biomasse que *D. geminata* produit pourrait modifier les flux énergétiques du réseau trophique et l'ampleur des effets serait tributaire du pourcentage de recouvrement, de l'épaisseur et de la durée des proliférations (Bothwell & Spaulding, 2008; James, 2011).

2.5.1 Impacts des proliférations sur les communautés périphytiques

L'observation de micrographies électroniques de tapis de *D. geminata* a révélé que malgré l'importante biomasse causée par les tapis mucilagineux, la communauté algale n'est pas dominée par didymo en termes d'abondance relative (Spaulding & Elwell, 2007).

2.5.2 Modification de la structure et l'abondance de la communauté des larves d'insectes aquatiques par les proliférations

De nombreuses études ont démontré que didymo est susceptible d'altérer le fonctionnement de l'écosystème lotique en modifiant la répartition et l'abondance des macroinvertébrés benthiques (James, 2011), la principale ressource alimentaire des saumons juvéniles (Rader, 1997). Quelques études ont déterminé que la présence de la matrice mucilagineuse de *D. geminata* modifie la composition et la structure de la communauté benthique (Larson & Carreiro, 2008; Kilroy *et al.*, 2009; Gillis & Chalifour, 2010). En fait, l'objectif des travaux menés par Gillis et Chalifour (2010) était d'évaluer l'influence de cette diatomée sur les communautés de macroinvertébrés benthiques de la rivière Matapédia. À l'automne 2006, trois stations situées en amont des proliférations de didymo, mais potentiellement favorables à la croissance et à la prolifération de l'algue ont été échantillonnées. En 2007, ces stations présentaient des colonies actives de didymo. Une station témoin sur la rivière Causapscal a également été suivie en 2006 et 2007 où aucune prolifération n'a été observée. Les résultats ont révélé que l'arrivée de didymo a modifié significativement la distribution des familles de larves d'insectes aquatiques entre 2006 et 2007 pour deux des trois sites de la rivière Matapédia ($p < 0.001$). La proportion de proies à faible valeur nutritive tels que les chironomides ont été augmentée alors que celle des Éphéméroptères, Plécoptères et Trichoptères (EPT) ont été diminuée suivant l'incursion de didymo (Figure 2.4). La qualité de la base alimentaire, en terme d'énergie disponible aux niveaux trophiques supérieurs, semblerait donc réduite par la présence de *D. geminata* (Kilroy, 2006; Rost *et al.*, 2011).

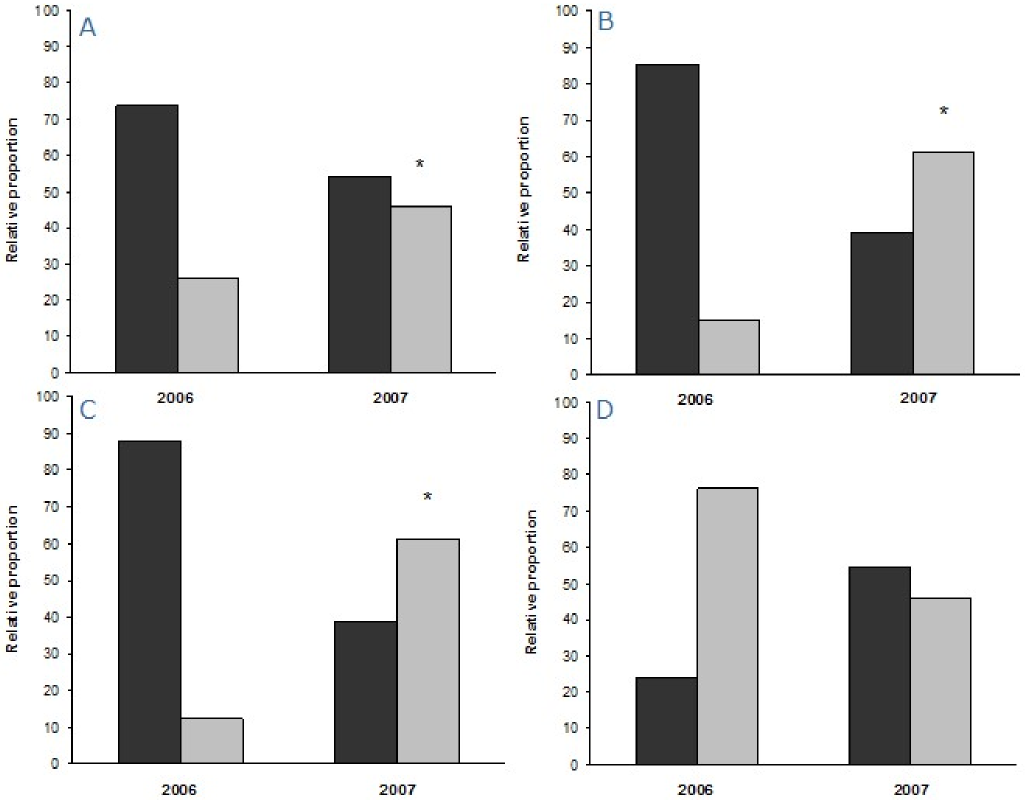

Figure 2.4 **Structure de la communauté de larves d'insectes aquatiques. Abondance relative des% EPT (noir) et % Chironomides (gris) entre 2006 (pré-didymo) et 2007 (post-didymo) de la rivière Matapédia (A, B, C) et Causapscal (D = témoin). La proportion de Chironomides est significativement différente (p = 0.01) suite à l'arrivée de didymo dans la rivière Matapédia (Gillis & Chalifour, 2010).**

En contrepartie, Gillis et Chalifour (2010) ont observé que la densité de larves prélevées est multipliée de quatre à cinq fois en présence de didymo ($p < 0.001$) (Figure 2.5). Les travaux de (Kilroy *et al.*, 2009) corroborent ces résultats.

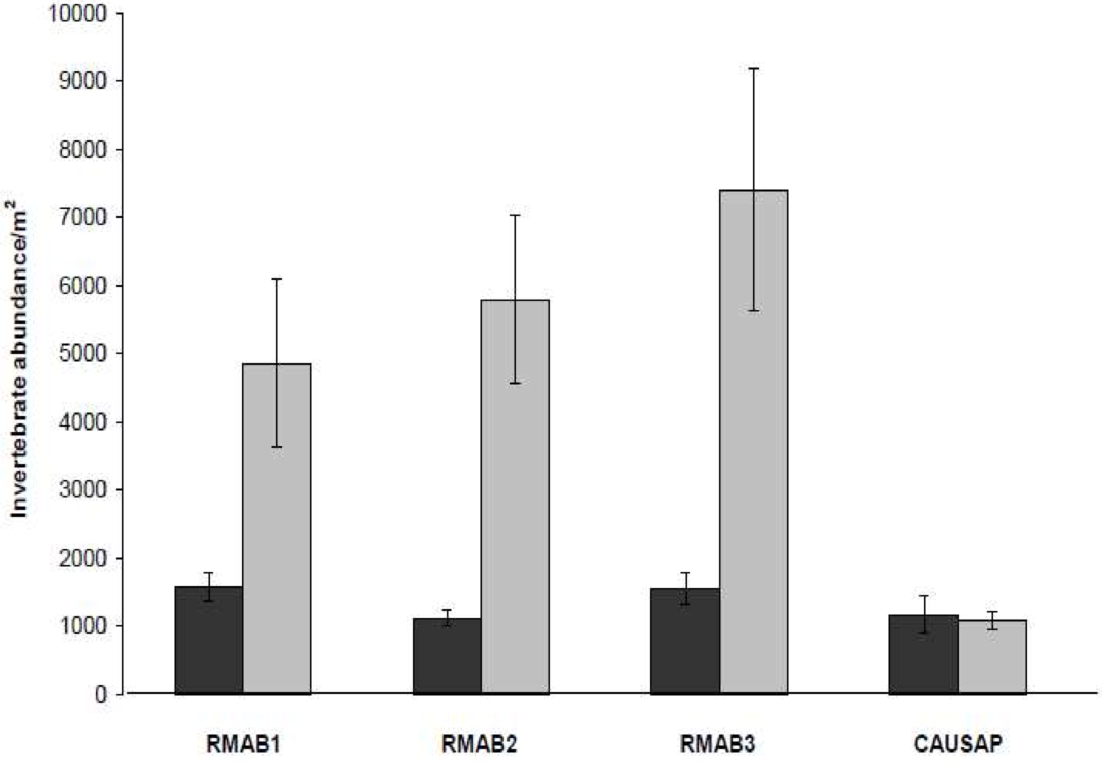

Figure 2.5 Densités de larves d'insectes aquatiques pré-didymo (noir) et post-didymo (gris) des rivières Matapédia et Causapscal (Gillis & Chalifour, 2010).

Sommairement, *D. geminata* peut former des tapis mucilagineux qui modifient drastiquement l'abondance et la proportion d'insectes aquatiques, principale ressource alimentaire pour les saumons juvéniles. Ainsi, la dynamique de la dérive de ces derniers doit être étudiée, et ce, en considérant la variabilité spatio-temporelle des proliférations.

Dérive des larves d'insectes aquatiques

L'augmentation de la densité des larves d'insectes aquatiques au sein des tapis ne signifie pas nécessairement que ces proies sont directement disponibles pour les salmonidés (Gillis & Chalifour, 2010). En fait, le tapis dense et fibreux de *D. geminata* pourrait limiter la dérive des larves d'insectes aquatiques et ainsi altérer la disponibilité des proies pour le saumon atlantique juvénile. Quelques études ont pourtant observé que la densité de dérive d'invertébrés était, au contraire, plus élevée en présence des proliférations abondantes de *D. geminata* (Shearer *et al.*, 2007; James, 2011). Les auteurs supputent que l'augmentation absolue de la densité d'invertébrés accroît, par le fait même, la densité de dérive. Toutefois, leurs analyses doivent être interprétées avec prudence puisque leur taille d'échantillon est petite et leurs efforts sont insuffisants pour évaluer l'effet de didymo sur la dynamique de la dérive (James, comm. pers).

2.5.3 Impacts sur l'écologie du saumon atlantique en rivière

L'ampleur des impacts de *D. geminata* sur le réseau trophique est largement méconnue à ce jour. Il n'existe actuellement aucune information rigoureuse permettant d'évaluer son impact potentiel sur les populations de saumon atlantique.

Comportement alimentaire

Aucune étude ne s'est attardée jusqu'à maintenant à la façon dont les poissons s'alimentent en présence de didymo. Afin de déterminer la portée réelle des impacts de didymo sur les salmonidés, il est essentiel de déterminer si le comportement alimentaire de ces derniers est modifié en présence de didymo. Chez le saumon atlantique juvénile, la quête de dérive est la principale méthode d'acquisition de la nourriture. Parfois, il effectuera des quêtes benthiques, c'est à dire des quêtes dirigées vers le lit de la rivière, afin de saisir une proie (Wańkowski & Thorpe, 1979; Stradmeyer & Thorpe, 1987). Toutefois, ce comportement survient rarement (Keeley & Grant, 1995) et l'alimentation benthique n'est généralement adoptée que lorsque la dérive d'invertébrés est limitée (Nislow *et al.*, 1998). Selon la théorie de la quête alimentaire des salmonidés, les taux de consommation sont étroitement corrélés avec l'abondance des proies. La diminution de la dérive provoquerait donc une modification du comportement par l'adoption d'un comportement de quête benthique (Nislow *et al.*, 1998). Puisque les salmonidés démontrent une plasticité de leur comportement alimentaire en réponse aux changements dans l'abondance de la nourriture (Dill, 1983), il est crucial de lier la disponibilité des proies à la diète afin de discerner les mécanismes modifiant la quête alimentaire, la croissance et la survie des saumons juvéniles (Nislow *et al.*, 1998). Théoriquement, la quête benthique est considérée comme étant plus énergivore que la quête de dérive (Godin & Rangeley, 1989) ce qui pourrait diminuer la profitabilité de l'alimentation lorsque didymo est présente (Shearer *et al.*, 2007). De plus, si les juvéniles adoptent un comportement de quête benthique, leur efficacité de quête alimentaire sera possiblement limitée par le recouvrement algal qui rendra plus difficile l'accès aux proies (Kilroy, 2006; Shearer *et al.*, 2007). Ainsi, les taux de croissance des juvéniles pourraient être limités (Fausch, 1984; Shelby, 2006; Shearer *et al.*, 2007).

Les salmonidés possèdent des stratégies comportementales afin d'optimiser l'utilisation de la diversité spatiale présente au sein de leur habitat (Heggenes *et al.*, 1999). Ils choisissent un environnement dont les caractéristiques physiques offrent un compromis entre les gains énergétiques et les coûts associés au métabolisme, la croissance, la reproduction et la survie (Fausch, 1984). Pour un même individu, l'habitat préférentiel varie selon le stade de vie, la saison et la fonction à remplir (alimentation, reproduction, refuge) (Heggenes *et al.*, 2002). La sélection d'habitat d'alimentation des saumons juvéniles est définie par la disponibilité de la ressource alimentaire et les coûts liés à la nage (Heggenes, 1996). Selon la théorie de quête optimale (profitabilité), si la ressource alimentaire est modifiée, il est probable que la sélection d'habitat sera modifiée (Godin & Rangeley, 1989). En fait, lorsque la disponibilité des proies est réduite, la taille de l'habitat utilisé et la fréquence des déplacements sont augmentées puisque les saumons juvéniles tendent à maximiser leur bilan énergétique (Wańkowski & Thorpe, 1979; Stradmeyer & Thorpe, 1987; Vehanen, 2003). Par conséquent, si la profitabilité est réduite en présence de *D. geminata*, il est possible que les saumons juvéniles modifient leur stratégie de quête alimentaire.

Le taux de croissance est une composante principale de la condition physique de l'individu. Puisque les juvéniles tendent à optimiser leur croissance et leur survie, il est probable que leur taux de croissance soit directement lié à leur préférence d'habitat ainsi qu'à leur régime alimentaire (Hansen & Closs, 2009). Afin de dresser un portrait des répercussions de didymo sur ce salmonidé, il est nécessaire d'aborder le concept de la dépense énergétique associée au gain énergétique sans toutefois omettre la notion de « plasticité comportementale » en réponse à la présence des proliférations d'algue didymo, une lacune des modèles précédents (Shearer *et al.*, 2007; James, 2011). Quelques études ont tenté de vérifier l'impact de *D. geminata* sur le recrutement et la croissance de la truite (Bergey *et al.*, 2009; James, 2011). En Nouvelle-Zélande, un modèle bioénergétique dépendant de la dérive de larves d'insectes a été élaboré afin d'évaluer l'impact de l'algue didymo sur la croissance de la truite. La modélisation a permis de prédire que les taux de croissance potentiels seraient plus élevés en présence de *D. geminata* puisque la dérive des proies ne semblaient pas être limitée par celle-ci (Shearer *et al.*, 2007). Au Dakota du Sud, les modèles bioénergétiques prédisent que la croissance de la truite brune sera également positive en présence *D. geminata.* Les auteurs estiment que malgré la modification de la ressource alimentaire (invertébrés plus petits mais densité absolue accrue), le bilan énergétique net sera positif et favorisera la croissance des individus (James, 2011). D'autre part, Lindstrom et Skulberg (2008) et Jonsson *et al.* (2008) n'ont décelé aucun impact significatif de la présence de *D. geminata* sur l'état des stocks de saumon atlantique en Norvège et en Islande. Toutefois, ces études n'ont pas permis d'identifier clairement les mécanismes pouvant agir sur la dynamique trophique lorsque *D. geminata* est présente. À ce jour, aucune étude ne permet de lier le déclin notable des stocks ou la diminution de la condition physique des truites à un possible effet des proliférations d'algue didymo.

Signatures isotopiques

Les ratios isotopiques de C et N permettent de révéler les interactions et les flux énergétiques entre les niveaux d'un réseau trophique aquatique (Power & Dietrich, 2002). Les ratios isotopiques sont dits 'enrichis' ou 'appauvris' selon que nous sommes respectivement en présence d'une augmentation ou d'une diminution de la quantité d'isotopes lourds (Doucett *et al.*, 1996). Les ratios isotopiques permettent l'identification des sources d'énergie au sein d'un réseau trophique puisque qu'ils sont fixés lors de la photosynthèse et demeurent relativement inchangés entre chaque niveau trophique (DeNiro & Epstein, 1978). Une étude de l'impact de *D. geminata* sur les ratios isotopiques de chacun des niveaux trophiques a été réalisée au Nevada. Les analyses de ces ratios ont révélé que la présence des tapis de didymo perturbe la dynamique du réseau trophique en modifiant la source principale de contribution en carbone à l'écosystème (Rost, 2010). Ainsi, puisque la base de la ressource alimentaire est altérée en présence de *D. geminata* (Gillis & Chalifour, 2010), il est probable que la signature isotopique des saumons juvéniles soit également modifiée. De plus, selon Cunjak *et al.* (2005), la signature isotopique de poissons « mobiles » comme les saumons juvéniles devrait refléter leur déplacement en lien avec la quête alimentaire. Ce type d'analyse pourrait donc s'avérer intéressant pour l'évaluation de la qualité de la diète des saumons juvéniles en lien avec la présence-absence de *D. geminata*.

Reproduction

Puisque les proliférations de *D. geminata* peuvent densément tapisser le lit de la rivière, il était soupçonné que cette biomasse algale altère l'habitat physique des salmonidés par le remplissage des interstices du substrat de graviers, ceux-ci étant couramment utilisés comme refuges par les salmonidés juvéniles et comme substrat de fraie par les adultes (Campbell, 2005; Larned *et al.*, 2007). Toutefois, *D. geminata* ne semble pas interférer avec les activités de frai automnales puisque les événements de crue abondantes et la faible intensité lumineuse lors de cette saison limitent l'ampleur des proliférations algales à cette période de l'année (McLaughlin, 2009a). Bickel et Closs (2008) corroborent cette hypothèse puisque le recouvrement de *D. geminata* n’influence pas les concentrations d’oxygène, ni le gradient hydraulique vertical de la zone hyporhérique, préservant ainsi les conditions optimales pour le développement des œufs (Bickel & Closs, 2008). En outre, une étude menée en Nouvelle-Zélande a démontré que la présence de l’algue didymo n’affectait pas la sélection des sites de frai des salmonidés (Shearer *et al.*, 2007).

2.6 Impacts de l’algue didymo sur l’économie locale

En raison de l’aspect visuel rébarbatif des proliférations de *D. geminata*, la valeur esthétique et économique des rivières touchées risque d’être négativement affectée. En fait, il a été constaté que la qualité de pêche laisse à désirer lorsque didymo est présente (Beville *et al.*, 2012). Beville *et al.* (2012) ont réalisé un sondage auprès des pêcheurs sur les habitudes de pêche en Nouvelle-Zélande. L’analyse des résultats a significativement démontré que la majorité des pêcheurs délaissaient les sites présentant des proliférations de *D. geminata*. L’effort de pêche et, par conséquent, les retombées économiques associées à cette activité récréotouristique, sont considérablement diminués (Branson, 2006; Beville *et al.*, 2012). En Nouvelle-Zélande, les pertes économiques liées à la présence de l’algue didymo ont été estimées entre $57 et 285 millions sur une période de huit ans (Branson, 2006). En Gaspésie, l’économie locale repose sur l’industrie de la pêche sportive au saumon (Lantz, 2010), d’où l’importance de s’attarder à l’étude de l’impact de la présence des proliférations de l’algue didymo sur cette ressource anadrome. En fait, lors des proliférations massives de 2006, *D. geminata* était si problématique que les gestionnaires s’ont vu forcé d’annuler quelques jours de pêche sportive.

CHAPITRE 3
RÉSUMÉ DES TRAVAUX DE RECHERCHE

Plusieurs travaux ont été effectués afin de répondre aux deux objectifs principaux de la recherche doctorale, soit, dans le volet 1, d'établir les causes de la prévalence de didymo dans les écosystèmes d'eau douce et dans le volet 2, de déterminer l'impact de sa présence sur le réseau trophique. Sept chapitres ont été rédigés en anglais sous forme d'articles scientifiques. Les chapitres 5 à 7 font partis du volet 1 alors que les chapitres 8 à 10 font partis du volet 2. Le chapitre 11, quant à lui, se veut une recommandation concernant la gestion de l'algue didymo tenant compte des avancées scientifiques réalisées au cours de la dernière décennie.

Le présent chapitre contient un résumé en français de chacun des articles scientifiques rédigés en anglais. Pour chacun de ces articles, l'ordre des auteurs est fonction de leur degré de contribution au travail réalisé et le détail de la contribution de la candidate est détaillé pour chacun des articles.

3.1 Un modèle conceptuel pour les proliférations et la persistance des tapis mucilagineux de la diatomée *Didymosphenia geminata* dans les cours d'eau oligotrophes (Chapitre 5)

James D. S. Cullis, Carole-Anne Gillis, Max L. Bothwell, Cathy Kilroy, Aaron Packman & Marwan Hassan

Contribution de la candidate

La candidate est deuxième auteure de l'article et a collaboré étroitement avec le premier auteur lors de la réalisation de toutes les étapes de l'article. Ses observations sur le terrain ainsi que sa connaissance exhaustive de la littérature lui ont permis de contribuer de façon importante au développement du modèle conceptuel. Elle a été impliquée dans toutes les étapes de la rédaction et révision du manuscrit ainsi que dans la préparation des figures et tableaux.

3.1.1 Introduction

Malgré le fait que l'algue didymo soit une problématique émergente à l'échelle planétaire, il existe une connaissance limitée de sa biologie et de son comportement en rivière. L'algue didymo, de par sa biologie, représente un paradoxe. Ceci est dû au fait que l'algue produit une importante biomasse mucilagineuse en eau froide, rapide et alors que les éléments nutritifs sont limités. Il n'existe aucune autre diatomée pouvant produire autant de biomasse si rapidement avec si peu de nutriments et pouvant persister dans un environnement lotique (Blanco & Ector 2009).

L'objectif principal de ce travail était de créer un modèle conceptuel des facteurs favorisant la formation et la persistance de didymo à partir d'une revue de littérature exhaustive suivie d'une synthèse des connaissances existantes sur l'algue didymo.

Le modèle conceptuel a été développé à l'été à 2010 dans le cadre de l'école d'été de l'Institut Hydrologique de Synthèse (HSSI) tenu à l'Université de la Colombie-Britannique (UBC) auquel la candidate a participé. Pendant deux semaines, un inventaire exhaustif des connaissances actuelles et des données disponibles concernant l'algue didymo a été effectuée. Les articles scientifiques, les rapports techniques et sommaires, les rapports réalisés par les instances gouvernementales des régions touchées ainsi que diverses thèses, ont fait l'objet de la revue de littérature nécessaire à la définition de l'assise du modèle. Au sein d'une équipe composée de quatre chercheurs et d'un autre candidat au doctorat, nous avons dressé les hypothèses et incorporé les observations respectives de chacune de nos régions. Les bases de données utilisées proviennent du Colorado (travaux de Cullis), de l'île de Vancouver (travaux de Bothwell), la Nouvelle-Zélande (Kilroy et Larned, NIWA) et du Québec (travaux de la candidate).

3.1.2 Le modèle conceptuel

Afin de développer le modèle conceptuel de l'algue didymo, il s'est avéré primordial de décrire les différentes phases dynamiques de la présence des proliférations en rivière : l'apport en cellules, la colonisation, la croissance et l'érosion des amas mucilagineux et la phase de recolonisation. Par la suite, il a été nécessaire de dresser la liste des facteurs pouvant régir chacune de ces phases dynamiques. Ces multiples facteurs de contrôle sont déterminés par des seuils dynamiques qui, ensemble, déterminent la fenêtre d'habitat de l'algue didymo.

La dynamique spatio-temporelle de l’algue didymo dépend de divers facteurs (ou conditions environnementales) dont les seuils critiques déterminent son comportement de prolifération. En rivière, la croissance d’algues benthiques est principalement déterminée par les variations saisonnières du débit, la température, la quantité de lumière reçue et la composition chimique de l’eau. Ainsi, ces facteurs ont été retenus comme ceux ayant le plus d’influence sur chacune des phases de croissance, et ce, tant pour la division cellulaire que la production de mucilage.

Les forces de cisaillement et le transport en charge de fond sont les principaux facteurs pouvant réduire et réguler la sévérité des proliférations. Afin d’être en mesure de coloniser ou recoloniser un milieu, l’habitat en rivière doit être adéquat à la survie de la cellule pour qu’elle puisse demeurer viable et se fixer sur le substrat. L’habitat en rivière doit également être adéquat à la production de mucilage. La fenêtre d’habitat, se veut donc une combinaison des seuils critiques des facteurs de contrôle (i.e. chimie de l’eau : pH et phosphore, température de l’eau, lumière (PAR), écoulement (τ)) constituant une fenêtre d’habitat à l’intérieur de laquelle la production de mucilage où la présence cellulaire est favorisée.

Puisque certains facteurs sont intrinsèquement liés et que l’importance relative de certains facteurs peut varier dans le temps et dans l’espace, la valeur des seuils critiques définissant la fenêtre d’habitat n’est pas définie. Toutefois, un résumé des intervalles de valeurs existantes extrait de la littérature a été réalisé. Les diverses lacunes ont été indiqués afin d’orienter les travaux de recherches futurs dans le but d’éventuellement améliorer le modèle conceptuel.

3.1.3 Discussion et conclusion

La fenêtre d’habitat pourra être utilisée dans un contexte de gestion de l’algue didymo. La connaissance des paramètres d’habitats favorables permet ainsi de déterminer si un bassin versant est sujet à la présence cellulaire de l’algue didymo et à la probabilité que l’algue puisse proliférer. Le modèle conceptuel, quant à lui, permet d’établir la variabilité et la sévérité saisonnière du comportement envahissant de l’algue didymo. D’autre part, dans le cas d’une rivière munie d’un barrage, des mesures de mitigation peuvent être entreprises par la création de crues soudaines créant un transport en charge de fond réduisant la biomasse algale.

3.2 Variabilité spatio-temporelle de la sévérité des proliférations de l'algue didymo à l'échelle du bassin versant (Chapitre 6)

Carole-Anne Gillis, Stephen J. Dugdale & Normand E. Bergeron

Contribution de la candidate

La candidate a déterminé les objectifs de recherche, a réalisé la recherche de financement, a développé le guide du bénévole, a effectué les formations des partenaires, le suivi avec les bénévoles, la validation des observations de terrain, ainsi que la gestion de la base de données. Elle a dirigé l'analyse des données, l'interprétation des résultats et la rédaction du manuscrit. Les co-auteurs ont soit été impliqués dans l'analyse des données ou la rédaction.

3.2.1 Introduction

Le bassin versant de la rivière Restigouche se situe à l'extrémité ouest de la péninsule gaspésienne (Figure 3.1). Il a une superficie totale de 12 780 km^2. Il est localisé à la frontière entre le Québec et le Nouveau-Brunswick, 8,6 % (6217,4 km^2) du bassin versant étant situé sur le territoire québécois contre 51,4 % (6562,7 km^2) sur le territoire néo-Brunswickois. Les bassins versants d'intérêt, soit où les proliférations d'algue didymo persistent depuis au moins 2007, sont ceux des rivières Upsalquitch, Patapédia, Matapédia, Causapscal et Milnikek.

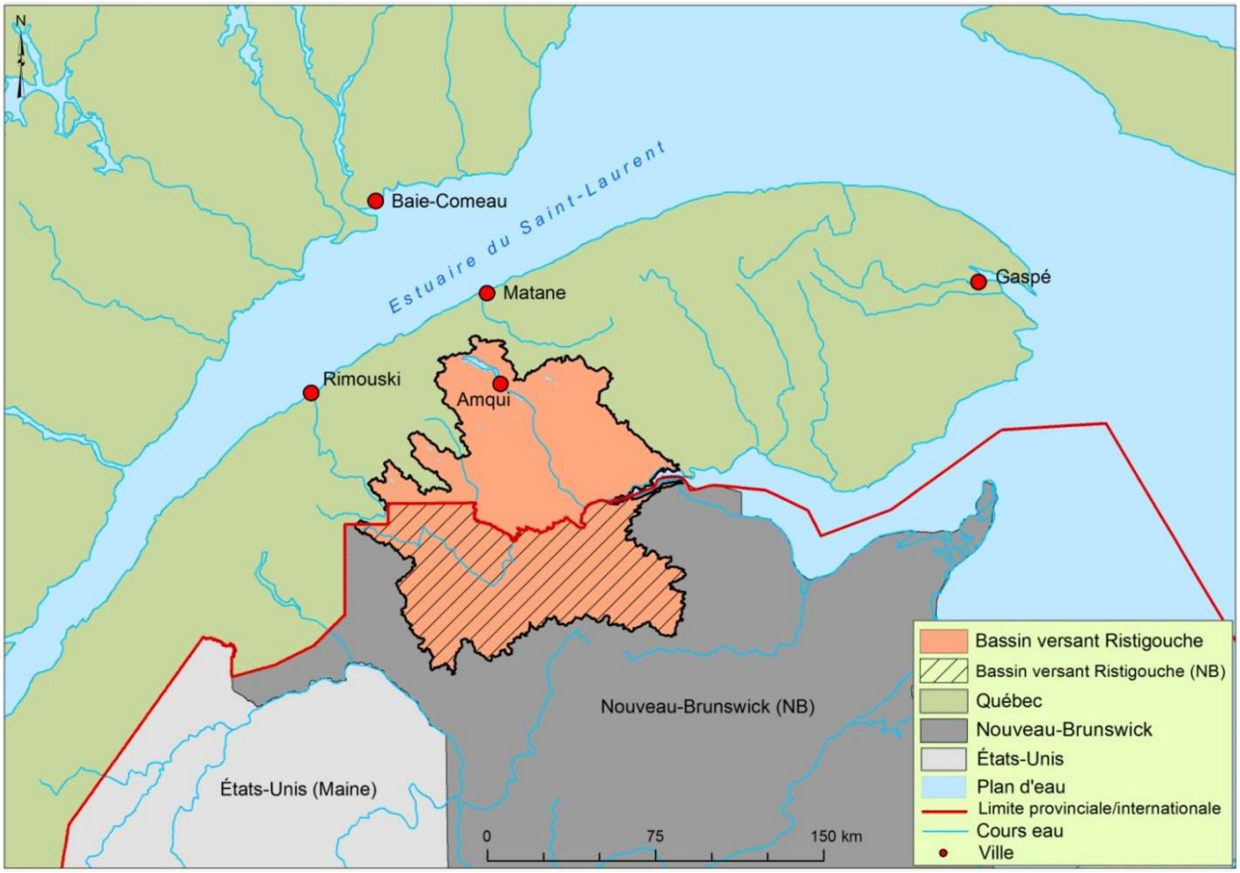

Figure 3.1 **Localisation du bassin versant de la rivière Restigouche. Source : Organisme de bassin-versant Matapédia-Restigouche.**

3.2.2 Matériel et Méthodes

3.2.2.1 Présence-absence des proliférations à l'échelle du tronçon

Un profil amont-aval des couples de faciès-substrat sur 65 km de la rivière Matapédia a été inventorié en 2007. Dans chacune des unités géomorphologiques, la présence-absence des proliférations de l'algue didymo était caractérisée.

3.2.2.2 Sévérité à l'échelle du bassin versant

En 2010, un réseau de surveillance des rivières constitué de citoyens a été mis sur pied afin de favoriser la collecte de données concernant l'évolution de la distribution géographique des proliférations. Les organisations liées à la ressource en eau, tels que les pourvoyeurs, les entreprises de location d'embarcation, les camps de pêche, les gestionnaires de rivières à saumon et les organismes de bassins-versants, ont été sollicités afin d'identifier les bénévoles permettant le suivi de la présence de l'algue didymo sur leur territoire. À chaque début de saison estivale, une formation de l'ensemble des employés de chaque organisation a été réalisée. Cette formation présentait la problématique de l'algue didymo, sa biologie, ses impacts potentiels ainsi que sa répartition géographique connue (Figure 3.2). Par la suite, afin de standardiser la collecte de données entre les observateurs, un guide de poche bilingue a été créé (Annexe 1). Ce guide fournit un répertoire photo présentant l'ampleur des proliférations permettant aux bénévoles d'indiquer le pourcentage de recouvrement observé en se basant sur ces photos. Le pourcentage de didymo est regroupé en cinq classes, par incrément de 20 % (Annexe 1). Des fiches d'observations étaient également fournies afin d'assurer que l'ensemble des informations pertinentes soient décrites par l'observateur (i.e. Nom de l'observateur, la date, la localisation, le pourcentage de recouvrement, l'épaisseur et l'aspect de la prolifération) (Annexe 1).

Figure 3.2 Formation de bénévoles du réseau de suivi volontaire. Source : Jordane Clermont.

Le réseau compte aujourd'hui plus de 70 bénévoles provenant de 22 organisations différentes qui recensent les proliférations des rivières du bassin versant de la rivière Restigouche.

La base de données générée a permis d'étudier les multiples mécanismes qui contrôlent la dynamique de la présence de l'algue didymo en fonction de différents paramètres d'habitat (i.e. intensité lumineuse, physico-chimie, substrat, faciès d'écoulement, etc.). Le réseau a également permis aux citoyens de collaborer concrètement à la recherche scientifique et d'augmenter le nombre de personnes sensibilisées à la problématique.

Afin de quantifier l'envergure des proliférations de *D. geminata* de manière standardisée, les observations ont été utilisées afin de calculer le Standing Crop Index (SCI) qui a été développé par Kilroy et Bothwell (2011). Cet indice considère à la fois l'épaisseur (mm) et le pourcentage de recouvrement algal sur un quadrat d'une surface de 1 m^2 dans la détermination de la valeur de l'index.

$$SCI = épaisseur \times \% \, de \, recouvrement$$

Par exemple, sur un tronçon recouvert à 50% de didymo et dont l'épaisseur moyenne des proliférations est de 20 mm, la multiplication de ces valeurs correspondra à 1000, soit la valeur du SCI à cet endroit (Figure 3.3).

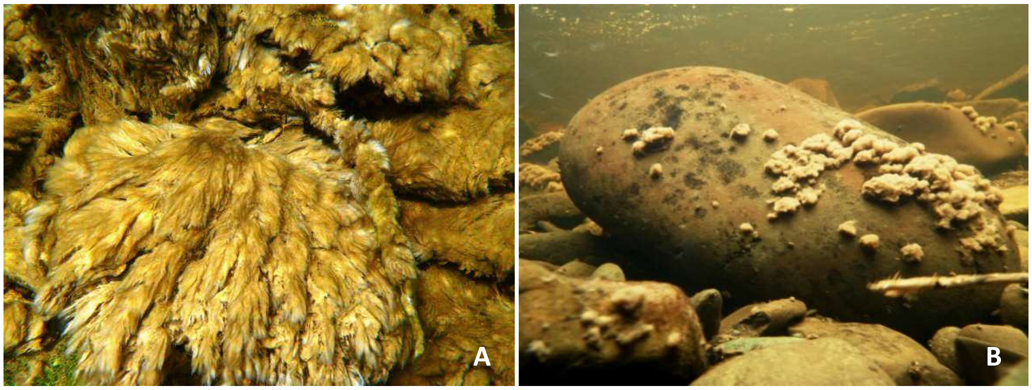

Figure 3.3 Exemples supplémentaires de SCI contrastants. A) 95% de recouvrement x 20 mm d'épaisseur, SCI=1900. B) 15% de recouvrement x 7 mm d'épaisseur, SCI=105.

3.2.3 Résultats

3.2.3.1 Présence-absence des proliférations à l'échelle du tronçon

Les résultats ont démontré que l'algue didymo se retrouvait plus fréquemment dans les seuils en comparaison aux autres types de faciès d'écoulement tels que les fosses, rapides et les chenaux ($\chi^2_{(3,\ N= 276)}$, $p < 0.05$). Toutefois, la taille de substrat au sein des seuils n'avait pas un effet significatif sur la présence-absence des proliférations ($\chi^2_{(3,\ N= 123)}$, $p > 0.05$).

3.2.3.2 Sévérité à l'échelle du bassin versant

Entre 2010 et 2015, 1 228 observations ont été effectuées par le comité de bénévoles. Dans un premier temps, nous avons classé les proliférations en trois catégories de sévérité en fonction de l'index SCI (Faible < 200 ; Modéré 200-600 ; Élevé > 600) dans un système d'information géographique. Six cartes présentant la sévérité moyenne annuelle des proliférations de l'algue didymo ont été générées pour l'ensemble du bassin versant. De toutes les variables hydrologiques analysées, nous avons identifié le débit maximal printanier comme celle ayant la plus forte influence négative sur la sévérité de l'algue didymo (KS test: $p < 0.05$). De plus, le débit maximal printanier explique à lui seul 71% de la variabilité de la sévérité des proliférations à l'échelle du bassin versant ($p < 0.05$).

3.2.4 Discussion et conclusion

Les données récoltées dans la cadre de ce projet ont permis d'identifier les facteurs de contrôle les plus déterminants à l'échelle du tronçon (faciès d'écoulement) et à l'échelle du bassin versant (débit). La création du réseau de suivi a permis de récolter une quantité importante d'observations décrivant la sévérité des proliférations de l'algue didymo à l'échelle du bassin versant. Le temps et l'effort consacré à la formation des bénévoles ont abouti à un vaste ensemble de données d'observations fiables qui n'auraient pas pu être obtenues autrement par le biais d'un programme de suivi conventionnel. Initié en 2010, ce réseau constitue le premier effort de suivi de l'algue didymo par le public.

3.3 Facteurs physico-chimiques régissant la présence-absence de l'algue à l'échelle régionale (Chapitre 7)

Carole-Anne Gillis, Rachel Gabor, James D.S. Cullis

Contribution de la candidate

La candidate a déterminé les objectifs de recherche et développé les hypothèses de recherche. De plus, elle a rassemblé l'ensemble des données disponibles provenant de diverses sources et organisé la base de données. Elle a également joué un rôle important dans l'analyse des données, l'interprétation des résultats et la rédaction de l'article. Les co-auteur(e)s de l'article ont contribué à l'analyse des données et la rédaction.

3.3.1 Introduction

L'objectif principal de ce chapitre était d'identifier les facteurs physico-chimiques contrôlant la biogéographie de l'algue didymo à l'échelle de l'est du Québec. Ainsi, une comparaison des données de divers paramètres physico-chimiques pouvant limiter la survie, la colonisation et la croissance de l'algue didymo à l'échelle régionale a été réalisée.

3.3.2 Matériel et Méthodes

3.3.2.1 Discerner les facteurs déterminant la biogéographie de l'algue didymo

Une analyse statistique des bases de données physico-chimiques historiques du MDDELCC (Banque de données sur la qualité du milieu aquatique) de 29 rivières à saumon du Québec a été effectuée afin d'identifier les paramètres limitant la colonisation et la croissance de *D. geminata*. Trente paramètres physico-chimiques ont été retenus pour l'analyse de données. Dans un premier temps, une comparaison de la physico-chimie de l'eau des régions touchées par *D. geminata* (Gaspésie et Bas-St-Laurent) et de celles exemptes de proliférations (Côte-Nord) a été effectuée afin d'identifier les paramètres qui favorisent ou nuisent à la survie des cellules de l'algue didymo.

De plus, une analyse en composantes principales (ACP) a été réalisée sur cette même base de données afin de vérifier la concomitance des principaux facteurs de contrôle physico-chimiques de la présence-absence de didymo. Un modèle prédictif a également été créé.

3.3.3 Résultats

Les deux premières composantes expliquent plus de 82% de la variance totale des données, avec 67,47 % expliquée par PC1 et la deuxième composante principale représentant 15,37 %. Les résultats de l'ACP permettent d'établir que la présence de l'algue didymo dans un cours d'eau est favorisée par le calcium, le carbone inorganique, l'azote total, la conductivité, les sulfates et le sodium. Inversement, sa présence est défavorisée par le fer et le carbone organique dissous.

Le modèle de régression logistique combiné de PC1 et PC2 n'a pas convergé et a permis de définir PC1 comme composante expliquant la plus grande variabilité de la distribution de l'algue didymo, alors que le rôle de PC2 n'était pas significatif. La régression logistique de PC1 a convergé (score de Fisher = 25 ; AIC = 4) et permet d'obtenir une probabilité binaire qu'une rivière donnée puisse favoriser ou non la survie et la colonisation de l'algue didymo.

3.3.4 Discussion et conclusion

Cette analyse des paramètres physico-chimiques permet de contribuer aux connaissances sur l'algue didymo par l'identification des facteurs régissant sa distribution à l'échelle régionale. Nos résultats démontrent que les rivières de la Côte-Nord ne sont pas favorables à la survie des cellules de l'algue didymo, ni à sa colonisation ou croissance puisque le pH < 7.0 et que la concentration en calcium est < 2mg L^{-1}.

La biogéographie de l'algue didymo est dépendante de l'échelle spatiale. En comparant les rivières situées au nord et au sud du Fleuve St-Laurent, la physico-chimie étroitement liée à la géologie était le facteur le plus déterminant de la présence-absence des cellules d'algue didymo. Toutefois, il est à considérer que lorsque nous comparons les rivières du Bas-St-Laurent à celles de la Gaspésie, l'absence des proliférations dans les rivières du Bas-St-Laurent semble être associée à la concentration plus élevée en nutriments qui limiterait la croissance des tapis.

Nos résultats permettent de définir que la distribution actuelle de l'algue didymo dans l'est du Canada est davantage liée aux paramètres définissant sa fenêtre d'habitat que la propagation des cellules de rivière en rivière.

3.4 Étude préliminaire de l'impact de la présence des proliférations de l'algue didymo sur la structure et la diversité des communautés périphytiques dans le bassin versant de la rivière Restigouche (Chapitre 8)

Carole-Anne Gillis & Isabelle Lavoie

Contribution de la candidate

La candidate a déterminé les objectifs de recherche, collaboré au devis du plan d'échantillonnage, et réalisé la planification des travaux terrain. De plus, elle a réalisé le travail de terrain et la collecte de données. Les analyses en laboratoire ont été réalisées par la co-auteure. La candidate a participé à l'analyse des données, à l'interprétation des résultats et à la rédaction.

3.4.1 Introduction

Dans le cadre du deuxième volet de recherche portant sur l'évaluation de l'impact de la présence des proliférations sur le réseau trophique, une étude a été réalisée afin de déterminer l'ampleur de l'impact des tapis fibreux sur la structure et la diversité des diatomées en rivière.

Lorsque l'algue didymo sécrète les tubes mucilagineux, ces derniers peuvent tapisser le lit de la rivière. La structure dense et fibreuse crée alors un environnement physique dans lequel les détritus et plusieurs diatomées peuvent se loger. Il a déjà été démontré que certaines diatomées peuvent se fixer aux tubes mucilagineux de la même manière qu'à un substrat.

Peu d'études se sont cependant penchées sur le sujet. Les deux objectifs spécifiques de cette étude étaient de 1) Comparer la structure de la communauté algale en présence et en absence de l'algue didymo et 2) Évaluer si l'augmentation de la complexité du biofilm (épaisseur du tapis algal) accroît l'ampleur de son impact sur les communautés algales.

3.4.2 Matériel et Méthodes

Deux échantillonnages des communautés périphytiques ont été réalisés pour répondre à chacun des objectifs. En 2010, deux échantillons composites ont été prélevés sur la rivière Patapédia, un composant le biofilm avec présence d'amas de l'algue didymo (SCI : 500-800) et l'autre composant le biofilm en absence d'amas (SCI : 0). Quatre échantillons ont ensuite été récoltés dans le Ruisseau Gagnon. Deux échantillons du biofilm avaient un SCI de 600 alors que deux autres échantillons avaient un SCI de 1300. Les résultats préliminaires de ce premier effort d'échantillonnage au ruisseau Gagnon ont permis d'indiquer que des données supplémentaires étaient nécessaires afin de tenter de répondre au deuxième objectif. Ainsi, en 2013, six sites additionnels ont été échantillonnés par sites appariés dans la rivière Patapédia, la rivière Restigouche et le ruisseau Gagnon. À chacun des sites, six surfaces d'échantillonnage ont été standardisées et le SCI de l'échantillon a été déterminé. Ces 36 échantillons ont été préservés avec une solution de Lugol. En laboratoire, chaque échantillon a été homogénéisé et nettoyé pour effectuer les analyses au microscope. Un minimum de 400 diatomées a été identifié afin de déterminer l'abondance relative de chacun des taxons. L'indice de diversité taxonomique Shannon a été calculé et diverses analyses statistiques ont été menées.

3.4.3 Résultats

Il est à noter que dans tous les échantillons, l'algue didymo représentait moins de 2% d'abondance relative. Dans le cadre du premier objectif, l'analyse des données récoltées à l'été 2010 a permis de caractériser la structure de la communauté algale en présence et en absence de l'algue didymo. Indépendamment de la présence de tapis d'algue didymo, l'abondance relative d'*A. minutissimum,* soit *le* taxon le plus abondant, était similaire entre les deux échantillons. La présence de l'algue didymo a quelque peu favorisé la richesse taxonomique, soit 21 taxons comparativement à 19 en son absence et un indice de diversité de Shannon de 1,46 comparativement à 1,38.

Dans le cadre du deuxième objectif, en comparant les échantillons du Ruisseau Gagnon de 2010 dont l'indice SCI était contrastant, la structure taxonomique entre les échantillons était divergente. Les échantillons provenant d'une épaisseur de tapis algal plus importante (SCI : 1300) possédaient une diversité taxonomique plus grande avec 21 taxons, que l'échantillon de biofilm mince (SCI : 600) avec 13 taxons. Pour chacun des échantillons récoltés en 2013 sur les six sites, six classes de sévérité ont été définies, 1 étant le SCI le plus élevé et 6 étant le SCI le moins élevé. La même tendance a été observée au niveau de la diversité taxonomique, lorsque la sévérité des proliférations de l'algue didymo augmente (épaisseur de son tapis mucilagineux), la diversité taxonomique des diatomées augmente. Une analyse ANOVA a toutefois déterminé que cette tendance était non significative. Néanmoins, la structure de la communauté algale est différente entre les classes de sévérité. Plus l'épaisseur du tapis est importante plus l'abondance des espèces fragilariés est importante. Selon l'indice de similarité Bray-Curtis, nos résultats démontrent que la variabilité de la structure taxonomique des échantillons est davantage liée au site d'échantillonnage qu'au niveau de sévérité des proliférations de l'algue didymo. Nous avons également comparé à l'aide d'un test de *t* les structures taxonomiques des échantillons de classe 6 (plus faible SCI) avec ceux de classes 1-5 (SCI plus élevé) afin de déterminer si la simple présence de tapis avait un impact sur les communautés périphytiques. La comparaison de l'indice Bray-Curtis de la classe 6 est significativement différente à l'indice des classes groupées ($t = 3.25$; $p < 0.01$) indiquant une modification de la structure taxonomique algal par la présence des proliférations.

3.4.4 Discussion et conclusion

Les espèces de diatomées observées dans nos échantillons sont similaires aux espèces répertoriées dans d'autres études nord-américaines. En concordance avec la littérature, malgré que le biovolume de l'échantillon soit composé à plus de 80% d'algue didymo, la faible abondance relative du nombre de cellules d'algue didymo dans les échantillons est due au fait que l'algue produit une quantité importante de mucilage. De plus, les cellules sont très larges comparativement aux autres diatomées qui dominent numériquement les échantillons. Nos résultats confirment que l'algue crée un habitat de choix pour les plus petites diatomées favorisant ainsi une plus grande diversité taxonomique. De ce fait, nos résultats démontrent que l'algue didymo n'homogénéise pas les communautés algales ni ne conduit à l'exclusion de taxons lorsqu'elle prolifère, telle une recherche précédente l'avait suggéré. Aussi, malgré une augmentation de la complexité du biofilm suivant son épaississement, il n'y a pas d'impact supplémentaire sur la structure et la diversité taxonomique des échantillons. La simple présence des tapis de didymo, soit dès la classe 5, occasionne un impact sur la structure et la diversité taxonomique des communautés périphytiques.

En conclusion, la structure de la communauté algale en présence de l'algue didymo diffère de celle lorsqu'elle est absente et l'augmentation de la complexité du biofilm (épaisseur du tapis algal) n'accroît pas l’ampleur de son impact sur les communautés algales. Ceci constitue la première étude ayant vérifiée l’impact des proliférations de l’algue didymo sur la communauté algale dans l’est du Canada.

3.5 Évaluation de l’impact des proliférations de didymo sur le comportement alimentaire du saumon juvénile (Chapitre 9)

Carole-Anne Gillis & Normand E. Bergeron

Contribution de la candidate

La candidate a déterminé les objectifs de recherche, a réalisé la recherche de financement, a élaboré les devis ainsi que la planification des travaux sur le terrain et en laboratoire. Elle a réalisé le travail de terrain et la collecte de données, l’analyse de ces dernières, l’interprétation des résultats et la rédaction de l’article. Le co-auteur a participé à l’analyse des données et à l’interprétation des résultats. Il a aussi collaboré à l’écriture.

3.5.1 Introduction

Puisque la structure de la communauté benthique est modifiée par la présence des proliférations de l’algue didymo et que les organismes benthiques constituent les principales proies des saumons atlantique juvéniles, l’objectif de ce chapitre était de vérifier l’impact de didymo sur le comportement alimentaire de ces derniers. De plus, nous voulions valider si la présence des tapis fibreux limitait la dérive, soit les proies disponibles aux saumons juvéniles.

3.5.2 Matériel et Méthodes

Des observations de comportement alimentaire ont été effectuées dans six sites de la rivière Patapédia présentant des pourcentages de recouvrement algal variant entre 0 et 85%. Entre juin et juillet 2010, la description du comportement de 49 juvéniles 0^+ a été réalisée par observations en apnée selon un protocole adapté de Dionne et Dodson (2002). L’observation du comportement alimentaire était réalisée entre 0800 h et 1700 h, soit lorsque les 0+ sont reconnus pour être très actifs (Nislow *et al.*, 1998). À chacun des sites, l'observateur (la candidate) débutait la séance d'observation par l'aval de la section et se dirigeait vers l'amont tout en réalisant des transects perpendiculaires à la berge. Une distance minimale de 1,5 m était respectée entre l'observateur et le poisson afin de ne pas influencer le comportement de ce dernier (Figure 3.4) (Cunjak & Power, 1986). Lorsqu'un poisson était repéré, celui-ci était observé pendant 1 minute afin de s'assurer que son comportement n'était pas influencé par la présence de l'observateur (Dionne & Dodson, 2002).

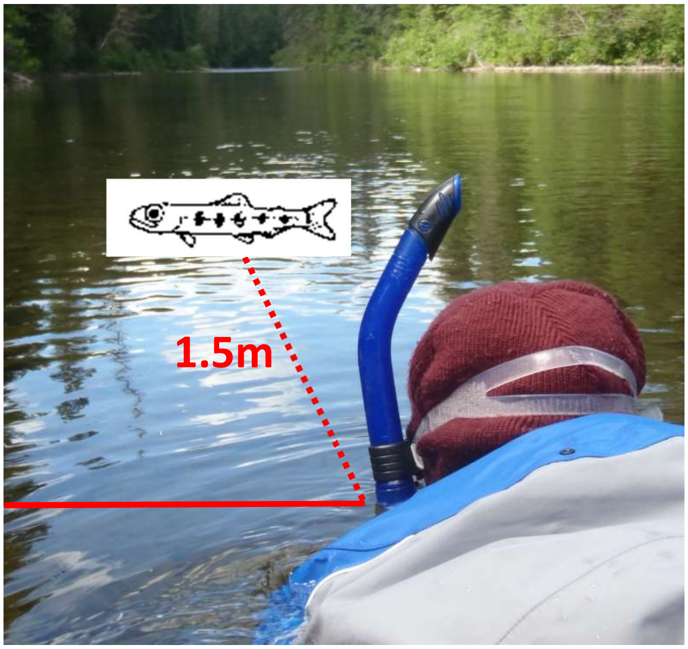

Figure 3.4 **Observation en apnée des saumons juvéniles. L'observateur est à l'aval de l'individu en respectant une distance de 1,5 m en demeurant perpendiculairement à la berge.**

Par la suite, l'ensemble des comportements du poisson étaient répertoriés sur une période d'observation de 15 minutes alors que l'observateur demeurait immobile. Les comportements (déplacement, stationnaire, alimentation, refuge et territorialité) étaient décrits en discriminant la quête alimentaire en deux catégories, soit la quête de dérive et la quête benthique. Chaque type de comportement correspondait à un code émis par l'observateur dans son tuba et sauvegardée à l'aide d'une enregistreuse. Lorsque la période d'observation de 15 minutes était complétée, un galet coloré était déposé à l'endroit où était situé le poisson afin d'effectuer ultérieurement des mesures d'habitat (vitesse, profondeur, substrat et pourcentage de recouvrement). De retour au bureau, ces données étaient ensuite analysées afin de déterminer, pour chaque individu étudié, le pourcentage de temps associé à l'alimentation et aux deux types de quêtes alimentaires, soit la quête benthique et la quête de dérive.

Des mesures de densités de dérive larvaire ont été effectuées à chacun des six sites de mesures du comportement alimentaire afin de déterminer si une éventuelle modification du type de quête en présence de didymo pourrait être associée à une altération de la densité de dérive larvaire.

À l'aval de chacun des sites d'études du comportement alimentaire, un filet de dérive (ouverture de maille 600 µm) a été installé afin de récolter la dérive pendant une période de 24 h précédant l'analyse du comportement alimentaire. La vitesse du courant était mesurée à l'installation ainsi qu'à la levée du filet afin d'obtenir une vitesse moyenne d'écoulement et ainsi mesurer le volume d'eau filtré par chacun des filets. Suite à la levée du filet, un échantillonnage composite (n=3) du benthos était réalisé à l'amont des filets de dérive afin de représenter la variabilité naturelle du benthos pouvant avoir dérivé vers le filet de dérive. Suite à la récolte des échantillons et leur identification en laboratoire, la densité de dérive (Dd) a été calculée en utilisant la formule :

$$D_d = \frac{100\,N}{3600\,t\,W\,H\,V}$$

où *N* correspond au nombre total d'individus; *t* le temps d'immersion du filet; *W* la largeur du filet, *H* la hauteur du filet et *V* la vitesse moyenne à 40% de la profondeur (Smock, 1996). La densité de dérive est donc standardisée en fonction du temps et de la vitesse (Hansen & Closs, 2009). Un total de 21 filets de dérive et échantillons de benthos ont été récoltés dans le cadre de cet objectif.

3.5.3 Résultats

Les chironomides et les éphéméroptères se sont avérés les proies les plus fréquentes dans les échantillons de dérive, et ce, dans tous les sites, indépendamment de la sévérité des proliférations au site d'échantillonnage. De plus, la densité de dérive n'était pas influencée par la sévérité des proliférations de l'algue didymo.

En ce qui a trait au comportement alimentaire, nous avons déterminé les coefficients de Spearman (ρ) et leurs probabilités respectives afin d'identifier les variables explicatives du modèle de régression multiple. Quatre paramètres ont été identifiés comme variables explicatives du comportement alimentaire observé, soient le pourcentage de recouvrement de l'algue didymo, la profondeur, la vélocité et la densité de dérive des proies. Une analyse utilisant la régression linéaire multiple « stepwise » par permutation a été réalisée afin de développer un modèle prédictif du comportement alimentaire. La première variable explicative, expliquant le plus grand pourcentage de variation du comportement alimentaire, est le pourcentage de recouvrement de l'algue didymo avec un R^2= 0,49 et un RMSE de 19,00 ($p < 0.001$). L'ajout de la deuxième variable prédictive, la densité de dérive des invertébrés, a permis d'améliorer le modèle avec un R^2= 0,54 et un RMSE de 17,87 ($p = 0.009$). La vélocité a été intégrée au modèle en tant que troisième variable explicative, et a amélioré le modèle, obtenant ainsi un R^2 = 0,60 et un RMSE de 16,53 ($p = 0.035$). La quatrième variable explicative, la profondeur, a été exclue du modèle puisque la relation entre le comportement alimentaire et la profondeur n'était pas significative. Ainsi, l'équation du modèle est la suivante :

% Quête benthique = 15,83 + % recouvrement (0,86) – Densité de dérive (0,51) + vélocité (0,38)

Ce modèle de régression logistique résultant permet de bien prédire le comportement alimentaire des saumons juvéniles.

3.5.4 Discussion et conclusion

Cette partie de la thèse a permis de démontrer que le saumon juvénile modifie son comportement alimentaire en présence de l'algue didymo. Alors qu'il s'alimente presqu'exclusivement sur la dérive en absence de didymo, le pourcentage de quête benthique augmente avec le pourcentage de recouvrement de didymo. Notre hypothèse initiale était que le comportement benthique devait être adopté car la densité de dérive serait limitée par les proliférations. Toutefois, nous n'avons trouvé aucune corrélation entre le pourcentage de recouvrement de l'algue didymo et la disponibilité des proies au niveau de la dérive.

Nous suggérons que la densité des proies benthiques augmente la profitabilité de la quête de benthique par rapport à la quête de dérive puisque les saumons juvéniles tendent à optimiser les gains énergétiques. Nous recommandons fortement que la densité de proies benthiques soit incorporée au modèle de régression multiple.

3.6 Évaluation de l’impact des proliférations de didymo sur la dynamique trophique et les répercussions prédateurs-proies (Chapitre 10)

Carole-Anne Gillis, Brian Hayden & Normand E. Bergeron

Contribution de la candidate

La candidate a déterminé les objectifs de recherche, a réalisé la recherche de financement, a élaboré les devis ainsi que la planification des travaux de terrain et en laboratoire. De plus, elle a réalisé le travail de terrain et la collecte de données, l’analyse de ces dernières, l’interprétation des résultats et la rédaction de l’article. Les co-auteurs ont participé à l’interprétation des résultats et à la rédaction.

3.6.1 Introduction

Afin d’évaluer l’impact des proliférations de l’algue didymo sur la diète du saumon atlantique juvénile, nous avons opté pour l’utilisation de l’analyse des isotopes stables au lieu de l’approche conventionnelle de l’analyse par contenus stomacaux. Les isotopes stables permettent d’intégrer la qualité et la composition de la diète sur de plus longues périodes que les contenus stomacaux. En fonction du renouvellement métabolique de différents tissus, tels que les muscles et les foies, il est possible d’inférer la variabilité temporelle de l’assimilation des signatures isotopiques des proies dans les tissus.

Ainsi, puisque la base de la ressource alimentaire est altérée en présence de *D. geminata* (Gillis & Chalifour, 2010), il est probable que la signature isotopique des saumons juvéniles soit également modifiée. L’objectif principal de ce chapitre était de caractériser la structure du réseau trophique ainsi que la modification de la qualité des proies disponibles au saumon juvénile en présence de didymo. Pour ce faire, nous avons échantillonné deux sites contrastés (0 % vs 90 % de pourcentage de recouvrement) et comparé diverses métriques trophiques, la contribution des proies à la diète des saumons juvéniles et leurs facteurs de condition physique.

3.6.2 Matériel et Méthodes

À chaque site, nous avons échantillonné le benthos ainsi que deux stades de vie du saumon juvénile (0+ et 1+). 17 échantillons composites d'invertébrés ont été groupés en trois groupes fonctionnels (prédateurs, détritivores et herbivores) alors que 78 échantillons de tissus de muscles et foies de saumons juvéniles ont été préparés. Nous avons préparé tous les échantillons en laboratoire et ils ont été analysés au SINLAB de l'Université du Nouveau-Brunswick. Par la suite, la correction lipidique mathématique a été appliquée aux signatures isotopiques de carbone pour les tissus de poissons.

3.6.3 Résultats

3.6.3.1 Modification de la diète du saumon atlantique juvénile par les proliférations de l'algue didymo

Le modèle bayésien MixSIAR permet de déterminer la contribution relative des différents groupes fonctionnels à la diète des saumons juvéniles. Dans le site présentant des proliférations, la signature isotopique des saumons juvéniles reflètent une diète appauvrie en carbone comparativement aux saumons juvéniles du site sans proliférations. Une comparaison statistique des signatures isotopiques des différents tissus par classe d'âge et par site a révélé que la diète des tacons est similaire à celle des alevins en présence de l'algue didymo (p = 0.301) alors qu'en son absence les tacons et les alevins ont une diète contrastée (p = 0.002). De plus, entre les sites, il y existe une différence significative entre les tissus et les classes d'âge.

Les saumons juvéniles, de par leurs signatures isotopiques des muscles, consommaient principalement des proies prédatrices, et ce, dans les deux sites. En contrepartie, la diète récente, représentée par les signatures isotopiques du foie, indique qu'au site témoin, les saumons juvéniles ont récemment consommé une plus grande proportion de proies herbivores alors que dans le site présentant des proliférations, les saumons juvéniles ont récemment consommé une plus grande proportion de proies détritivores.

3.6.3.2 Modification de la diversité trophique par l'algue didymo

Le programme SIBER permet d'extraire différentes métriques décrivant la structure du réseau trophique à chacun des sites. Ainsi, au site témoin, les saumons juvéniles ont une diète plus diversifiée et une niche trophique plus grande comparativement au site présentant des proliférations de l'algue didymo.

3.6.3.3 Répercussions sur la condition physique des saumons juvéniles

La condition physique des saumons juvéniles et les ratios C :N ne semblent pas être représentatifs de la qualité respective de la diète aux sites puisqu'il n'y a pas de différence significative entre les deux. Toutefois, la taille moyenne des individus est plus élevée dans le site témoin.

3.6.4 Discussion et conclusion

Les résultats de ce chapitre informent sur la modification saisonnière de la dépendance des ressources alimentaires, et ce, dans chacun des sites échantillonnés. Toutefois, la diète récente s'avère significativement différente entre les sites en raison de la présence des proliférations de l'algue didymo. Les saumons juvéniles y consomment des proies détritivores occasionnant ainsi une diète appauvrie. La niche trophique est également plus restreinte et les saumons juvéniles ont une diète moins diversifiée. Malgré cela, l'indice de condition physique et l'indice lipidique (C:N) n'en sont pas diminués en présence des proliférations de l'algue didymo. La taille moyenne des individus est toutefois plus grande dans le site témoin. Il serait pertinent de vérifier l'effet de l'algue didymo à l'aide d'acides gras, permettant ainsi une résolution plus fine à l'aide de nombreux biomarqueurs.

3.7 Défis liés à la gestion de l’algue didymo (Chapitre 11)

Leah C. Elwell, Carole-Anne Gillis, Lisa A. Kunza & Meg D. Modley

Contribution de la candidate

La candidate a étroitement collaboré avec les co-auteurs afin d’élaborer un article succinct et clair. Elle a participé à la revue de la littérature ainsi qu’à toutes les étapes de rédaction et de révision de l’article.

Résumé des recommandations

Lors de la conférence internationale de Didymo tenu à Providence Rhode Island au printemps 2013, les gestionnaires de rivières de plusieurs paliers gouvernementaux et organisations à but non-lucratif ont demandé conseil à la communauté scientifique internationale. Puisque l’algue *Didymosphenia geminata* est une problématique émergente dans nombreux pays, plusieurs chercheurs étudient la problématique dans leurs régions respectives. Au cours de la dernière décennie, plusieurs avancées ont été réalisées mais plusieurs efforts demeurent, notamment, à valider les seuils critiques du modèle conceptuel pouvant déterminer la présence-absence tant de cellules que des proliférations. Toutefois, malgré le statut de la recherche, il y a un urgent besoin de communiquer un message clair et consensuel aux gestionnaires de la part de la communauté scientifique.

Que l’algue soit considérée exotique, envahissante ou indigène, qu’elle soit propagée ou non, elle occasionne des perturbations aux écosystèmes en rivière. Et, peu importe l’étiquette qu’on associera à son statut dans une région donnée, la gestion des proliférations demeure la problématique collective.

Ainsi, la sensibilisation vis-à-vis le risque de propagation demeure le message clé à communiquer alors que la recherche scientifique se poursuivra concurremment : Vérifier, nettoyer, séchez ou congelez.

3.8 Liens entre les volets de recherche

Afin d’être en mesure d’étudier l’impact d’une espèce nuisible sur un écosystème donné, la compréhension des facteurs régissant sa présence et son abondance est essentielle. Seule la variabilité spatiotemporelle de la sévérité des proliférations de l’algue didymo déterminera l’ampleur de son impact sur l’écosystème.

C’est ainsi que cette thèse est structurée, soit en deux volets de recherche intrinsèquement liés l’un à l’autre puisque l’ampleur des proliférations, qui ultimement déterminera l’impact sur la structure et le fonctionnement du réseau trophique, dépend nécessairement des facteurs régissant l’épaisseur, le pourcentage de recouvrement et la durée des proliférations en rivière (Figure 3.5).

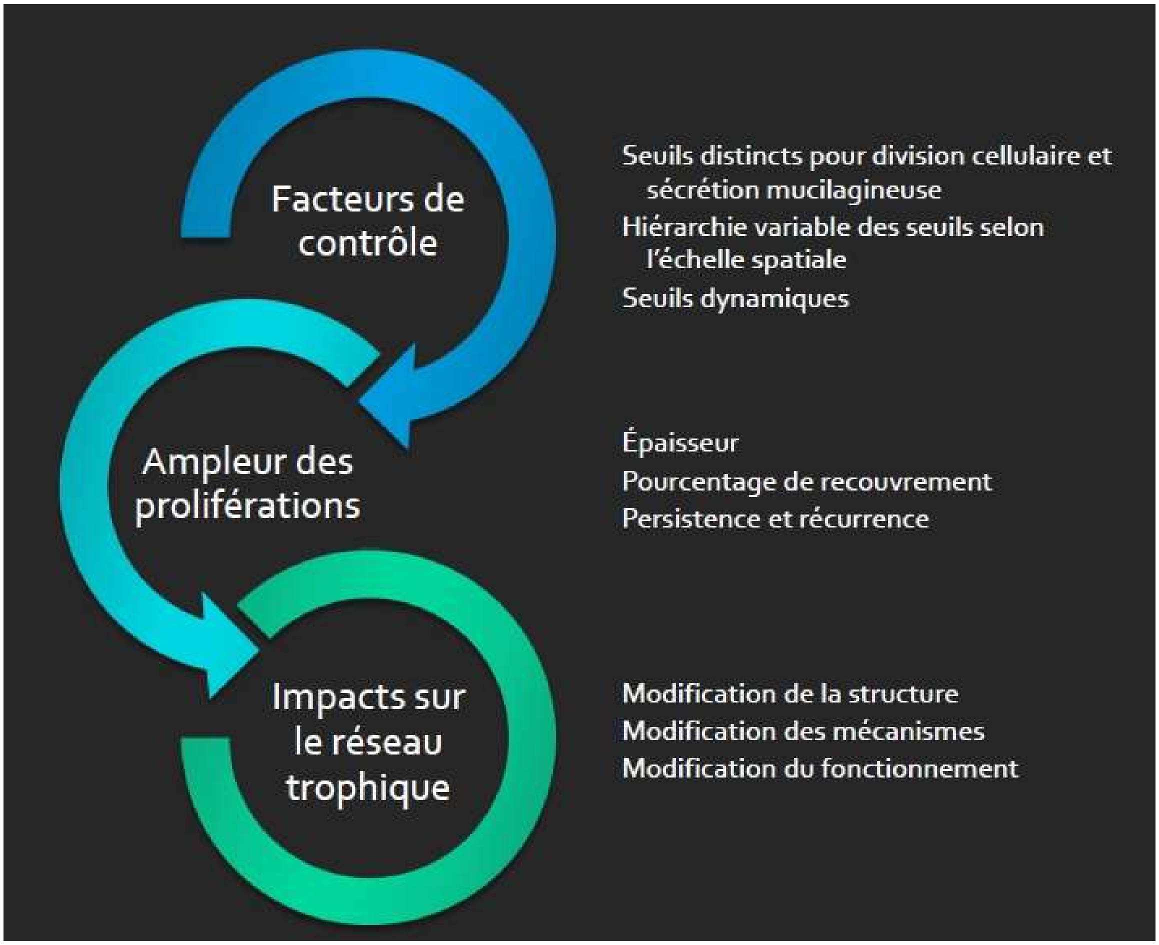

Figure 3.5 Schéma de l’interconnexion entre les facteurs de contrôle des proliférations (volet 1) et l’impact de ces dernières sur le réseau trophique (volet 2)

La contribution des articles au premier volet de recherche a permis de mettre en lumière la variabilité spatiotemporelle des seuils déterminant la présence-absence cellulaire mais également des seuils déterminants l'ampleur des proliférations. Le modèle conceptuel du Chapitre 5 est un outil évolutif par lequel la compréhension des divers mécanismes de contrôle peut être étudiée et améliorée. Dans la cadre de la thèse, le modèle conceptuel a été appliqué à diverses échelles spatiales. À l'échelle du tronçon, le faciès d'écoulement régit la présence-absence des proliférations (Chapitre 6) alors qu'à l'échelle régionale, ce sont les paramètres physico-chimiques qui déterminent sa biogéographie (Chapitre 7). La variabilité interannuelle des proliférations est principalement déterminée par l'intensité de la crue printanière (Chapitre 6). Les résultats de cette thèse contribuent au renforcement et à l'amélioration du modèle conceptuel.

Le degré de sévérité des proliférations, régit par les facteurs décrits précédemment, a une incidence sur l'ampleur des impacts de l'algue didymo sur la structure et le fonctionnement du réseau trophique. La contribution des articles au second volet de recherche a permis d'établir que les tapis denses et fibreux créent un habitat de choix tant pour les algues périphytiques que les macroinvertébrés détritivores. Toutefois, la modification de la structure et de la diversité des communautés basales par les proliférations provoque une altération de l'utilisation des ressources alimentaires des saumons juvéniles. Puisque ces derniers possèdent une plasticité comportementale, ils modifient leur quête alimentaire en réponse aux modifications de leur habitat. L'analyse des signatures isotopiques a révélé que la diète des saumons juvéniles est significativement modifiée en présence des proliférations, consommant des proies moins diversifiées et de plus faible valeur calorique. L'effet sur la condition physique de cette diète appauvrie sur les saumons juvéniles n'a toutefois pas été résolu.

CHAPITRE 4
CONCLUSION DE LA THÈSE

4.1 Contribution scientifique

Le mandat premier de cette recherche était de tenter de répondre aux multiples interrogations de la population locale dont les usages de la rivière ont été lourdement affectés par la présence de l'algue didymo. Les espèces à potentiel envahissant représentent une menace majeure à la biodiversité des écosystèmes aquatiques (Dudgeon *et al.*, 2006). Il a été primordial d'effectuer des travaux de recherche sur l'algue didymo puisque la problématique de ses proliférations est un phénomène relativement nouveau à l'échelle planétaire. Cette thèse constitue un pilier important dans l'acquisition de connaissances sur les facteurs régissant sa présence et ses impacts sur le saumon atlantique. Dans le cadre de ce projet de recherche, un réseau d'observateurs a été créé et grâce à cette approche a permis d'amasser des données de qualité sur la variabilité spatio-temporelle de l'algue didymo sur une période de six ans, alors que la majorité des études sur l'algue didymo ne porte que sur une période de deux ans.

Par la suite, quelques études sont en cours à l'international, mais très peu d'entre elles concentrent leurs efforts sur l'impact de la présence de didymo sur le réseau trophique. Le présent projet est le seul projet de recherche visant le saumon atlantique juvénile malgré plusieurs pays touchés par l'algue didymo et supportant des populations importantes de saumon atlantique tel que l'Islande, la Norvège et l'Écosse. De plus, l'intégration des volets « comportement alimentaire » confère un aspect très innovateur et inexploré à ce jour, une composante qui devra être incorporée dans les modèles bioénergétiques. Ce volet a permis d'identifier certains mécanismes régissant l'ampleur des impacts de cette algue sur le réseau trophique. L'utilisation du saumon atlantique comme espèce témoin permettra de transposer l'impact de l'algue didymo sur les niveaux trophiques supérieurs aux autres régions touchées et supportant des populations salmonicoles importantes. De plus, le projet défini les orientations de recherches futures afin d'identifier les facteurs qui déterminent l'ampleur des proliférations et leurs répercussions sur les écosystèmes lotiques.

4.2 Orientations de recherches futures

Plusieurs aspects de recherche ont été investigués dans le cadre de cette thèse, toutefois, afin de comprendre tous les mécanismes de l'impact des proliférations de l'algue didymo en rivière, plusieurs autres composantes de l'écosystème devront être incorporées dans le futur. Une approche multidisciplinaire sera de mise et une réplication des études dans diverses régions du globe permettra une généralisation des impacts et des mécanismes par lesquels l'algue didymo modifie le fonctionnement de divers écosystèmes aquatiques.

4.2.1 Facteurs de contrôle

Il est important de distinguer la division cellulaire et la production de mucilage. Les facteurs abiotiques régissant l'un peuvent ne pas régir l'autre (Cullis *et al.*, 2012). Pour ce qui est des facteurs de contrôle régissant la division cellulaire et la production de mucilage, la distribution précise de l'algue doit être connue à l'échelle à laquelle l'hypothèse de recherche sera vérifiée. La recherche concertée sur diverses échelles géographiques contribuera à la production d'un ensemble de données permettant une modélisation écologique plus précise de l'habitat préférentiel de l'algue didymo. Afin d'optimiser la détection de cette algue sur de grandes superficies, l'approche de détection par qPCR pourrait s'avérer utile afin de confirmer la présence-absence de l'algue didymo à l'échelle régionale, provinciale, nationale ou continentale (Kim-Tiam, 2017). Afin d'étudier davantage les facteurs de contrôle de la biogéographie de l'espèce, l'obtention de données sur les diverses variables explicatives devront coïncider avec les données de présence-absence et de sévérité des proliférations de l'algue didymo afin d'identifier l'importance relative de ces seuils à diverses échelles spatiales.

D'autre part, la dynamique temporelle des proliférations et les facteurs locaux influençant la saisonnalité de cette diatomée seront importants à définir. La température et la lumière demeurent des facteurs ayant reçu peu d'attention et il serait intéressant de valider les seuils critiques de ces derniers ainsi que leur concomitance avec la variable débit. L'utilisation de canaux expérimentaux peut s'avérer utile afin de tester divers seuils critiques d'écoulement et conditions physico-chimiques de l'eau. D'autre part, la mitigation des proliférations pourrait être réalisée lorsque les proliférations se situent en aval d'un barrage. Un relâchement d'un volume d'eau suffisamment important pour créer un transport en charge de fond permettra l'érosion et le décrochement des proliférations sur le lit.

De plus, Kuhajek et Wood (2014) ont récemment testé un large éventail de variables physico-chimiques en laboratoire. La continuité de ces travaux sera essentielle à la détermination de la valeur des seuils critiques pour chaque paramètre au sein du modèle conceptuel de la fenêtre d'habitat. La recherche sur les mécanismes par lesquels cette algue utilise les ions afin de produire de si grandes quantités de biomasse dans des eaux à faible en nutriments sera primordiale afin d'envisager des approches efficaces de mitigation.

4.2.2 Impacts sur le réseau trophique

Il a été démontré à plusieurs reprises que l'algue didymo modifie la structure de la communauté de macroinvertébrés benthiques. Toutefois, il sera nécessaire d'incorporer comment ces changements à la structure des communautés peuvent modifier les mécanismes et le fonctionnement de l'écosystème. Une approche combinée, visant à caractériser les détritus, la matière organique particulaire, la communauté algale, le benthos et la dérive de macroinvertébrés, les densités et la taille des poissons, les contenus stomacaux, le comportement alimentaire, les signatures isotopiques, et le contenu en lipides des proies et des consommateurs permettrait d'intégrer l'ensemble des modifications à la structure des communautés par l'algue didymo mais également d'identifier les mécanismes par lesquels l'algue didymo altère le fonctionnement de l'écosystème.

La recherche future devra viser à caractériser l'ampleur des impacts en fonction de la sévérité des proliférations (pourcentage de recouvrement, épaisseur et durée). En échantillonnant divers gradients de biomasse, il sera possible d'identifier un seuil critique de sévérité des proliférations qui engendrerait des impacts négatifs. Rost et Frietsen (2014) ont récemment suggéré, considérant l'ubiquité des proliférations à l'échelle planétaire, que la question de recherche pertinente passera de « est-ce que l'algue didymo est présente dans mon cours d'eau? » à « est-ce qu'il y a trop d'algue didymo dans mon cours d'eau? ».

4.3 Recommandations aux gestionnaires

Au cours de la dernière décennie, les gestionnaires se sont questionnés sur la dichotomie du statut exotique ou indigène de l'algue didymo. C'est également un débat d'actualité dans la communauté scientifique (Bergey & Spaulding, 2016; Taylor & Bothwell, 2016). Qu'elle soit identifiée comme « espèce exotique envahissante » ou non, l’algue didymo peut être propagée, a un comportement envahissant et est nuisible aux écosystèmes. L'ampleur des proliférations et leur récurrence ont une incidence sur la vitalité économique des rivières à saumon ainsi qu'un impact considérable sur l'écosystème.

Puisque l’algue didymo est un organisme microscopique pouvant être propagée par divers vecteurs, l’approche à privilégier est d’implémenter ou de maintenir un programme d’éducation aux usagers sur les risques de propagations des espèces nuisibles de concert avec des stations de nettoyage avec affichage mis à la disposition de ces derniers. La vulnérabilité de nos écosystèmes aquatiques à d’autres espèces exotiques envahissantes (EEE) est grande compte-tenu de l'achalandage touristique dans l’est du Québec.

Par conséquent, une approche proactive assurera un ralentissement de la propagation de l’ensemble des espèces aquatiques nuisibles. La stratégie préventive recommandée est de *vérifier, nettoyer, sécher, congeler* l’équipement ayant été en contact avec l’eau avant le déplacement vers un autre cours d’eau.

PARTIE 2

ARTICLES

CHAPITRE 5

A CONCEPTUAL MODEL FOR THE BLOOMING BEHAVIOR AND PERSISTENCE OF THE BENTHIC MAT-FORMING DIATOM *DIDYMOSPHENIA GEMINATA* IN OLIGOTROPHIC STREAMS

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Abstract

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.

5.1 Introduction

The functioning of stream ecosystems is maintained through a diversity of biotic and abiotic controls (Allan & Castillo, 2007) and complex physical and biological interactions (Hart & 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 & Hornberger, 2006).

The mat forming diatom *Didymosphenia geminata* (Lyngbye) M. Schmidt is growing in significance in its impact on lotic systems globally (Blanco & 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.

The objective of this paper is to present a conceptual model for the growth, persistence and blooming behavior of *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.

5.2 Background

5.2.1 Threat to the Sustainability of Stream Ecosystems

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 & 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 & Elwell, 2007) and habitat structure, and foodweb dynamics (Kilroy *et al.*, 2009; Gillis & Chalifour, 2010). 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.

5.2.2 Increasing global concern

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 & 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 & 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 & 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 & 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 (Spaulding & Elwell, 2007; Bothwell & Spaulding, 2008). 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 & Ector, 2009).

5.2.3 The Didymo Paradox

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 & 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 (Herath, 1997; Smith *et al.*, 1999; Anderson *et al.*, 2002;). *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.

5.3 Outlining a Conceptual Model Based on Threshold Dynamics

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.

A fundamental concept behind threshold behavior is that there are distinct modes of dynamic behavior at the macro-scale (Zehe & 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 & Sivapalan, 2009). Consideration of the different 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 5.1.

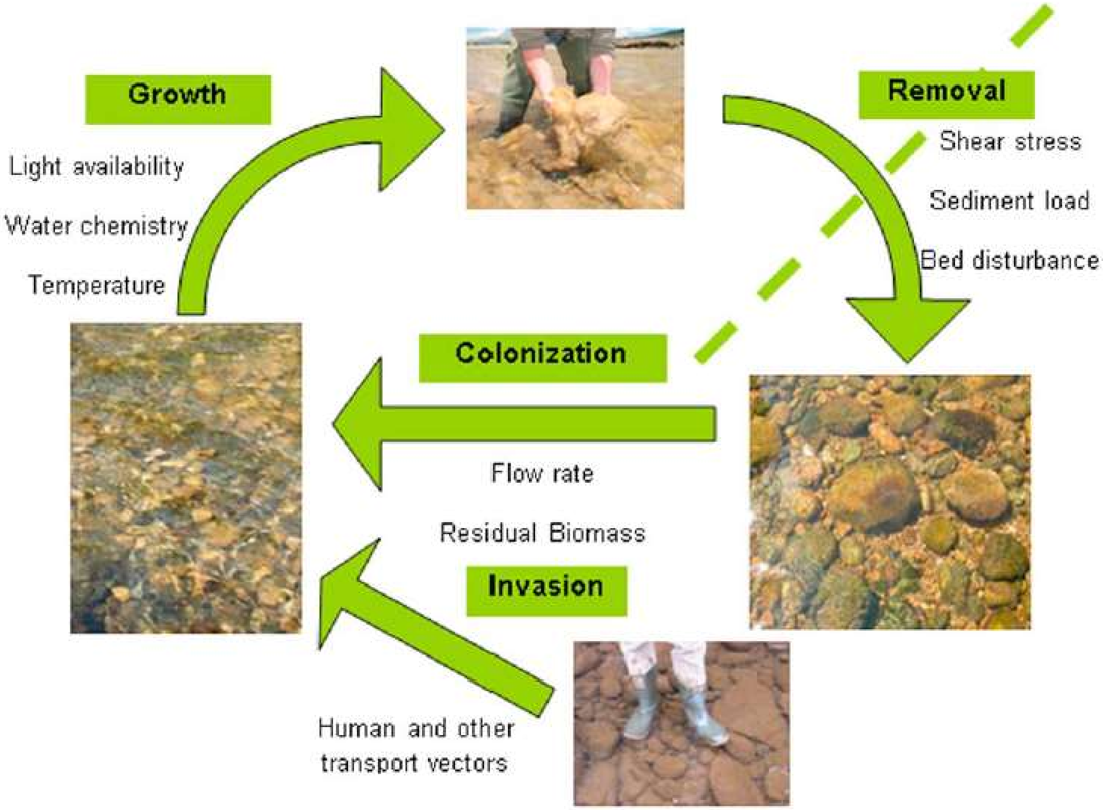

Figure 5.1 Proposed dynamic phases (in bold) for modeling the growth dynamics of *D. geminata* and the potentially significant controlling parameters for each dynamic phase

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 5.1 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 5.1 that involve linear as well as highly nonlinear response functions.

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 & McCutchan, 2010). Of these, flow variations is considered to be the master variable (Poff *et al.*, 1997). Figure 5.2 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-related disturbance event, and recolonization after the disturbance event. Although Figure 5.2 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.

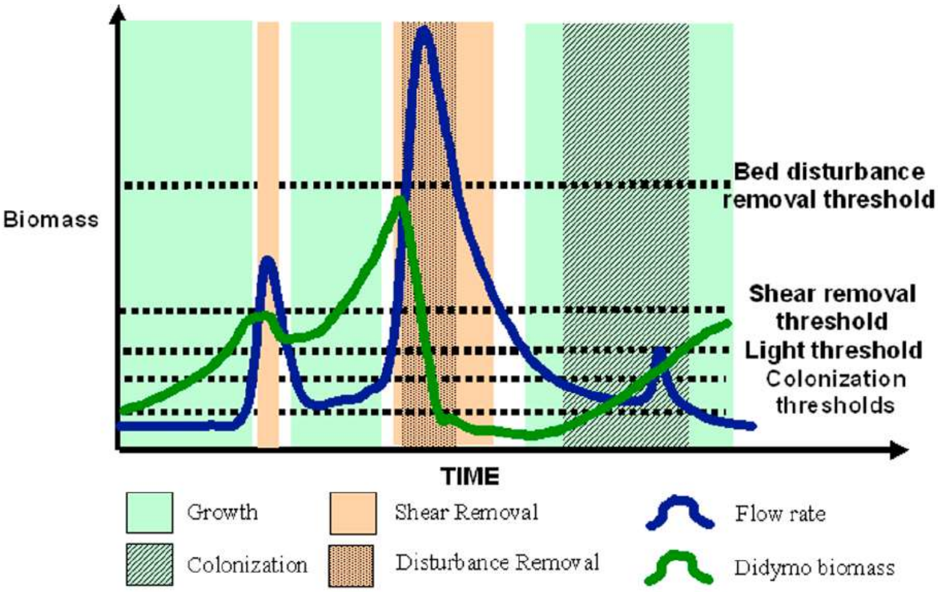

Figure 5.2 **Schematic representation of the relationship of various thresholds that may affect *D. geminata* mat growth/biomass under variable flow. Thresholds are ordered from lower flow (colonization thresholds, bottom) to higher flow (bed disturbance removal threshold, top).**

5.4 Invasion and Growth Defined by a Suitable Habitat Window

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.

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 & 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).

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 5.3.

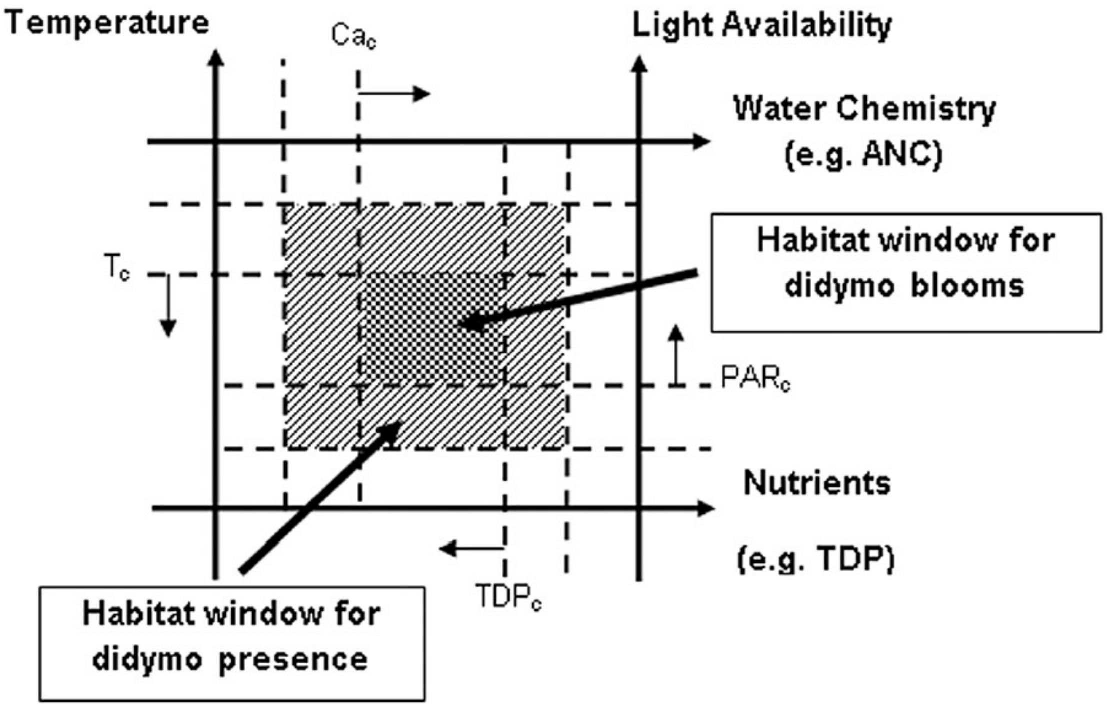

Figure 5.3 **Example of a proposed habitat window describing the potential for *D. geminata* to be present in a stream as well as the potential for nuisance blooms to form, as defined by a set of as yet unconfirmed and unknown potential critical threshold requirements for temperature (Tc), light availability (PARc), water chemistry represented by acid neutralizing capacity (ANCc), and nutrient concentrations (TDPc).**

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 habitat window. These include high light availability (Whitton *et al.*, 2009), low nutrient concentrations (Spaulding & 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 (PARc), critical nutrient concentration such as total dissolved phosphorus (TDPc), critical water chemistry characteristics such as Acid Neutralizing Capacity (ANCc) and critical temperature thresholds (Tc) as shown in Figure 5.3.

5.5 Shear Stress, Bed Disturbance, and the Scouring of Mats

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 mats is often defined in terms of a critical flow rate as flow is the most readily available hydraulic parameter (Poff & 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).

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 & 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 & 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 5.4 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 & Hauer, 2003), as shown in equation (1),

$$\tau_c = \theta_c(\rho_s - \rho_w)gD$$

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.

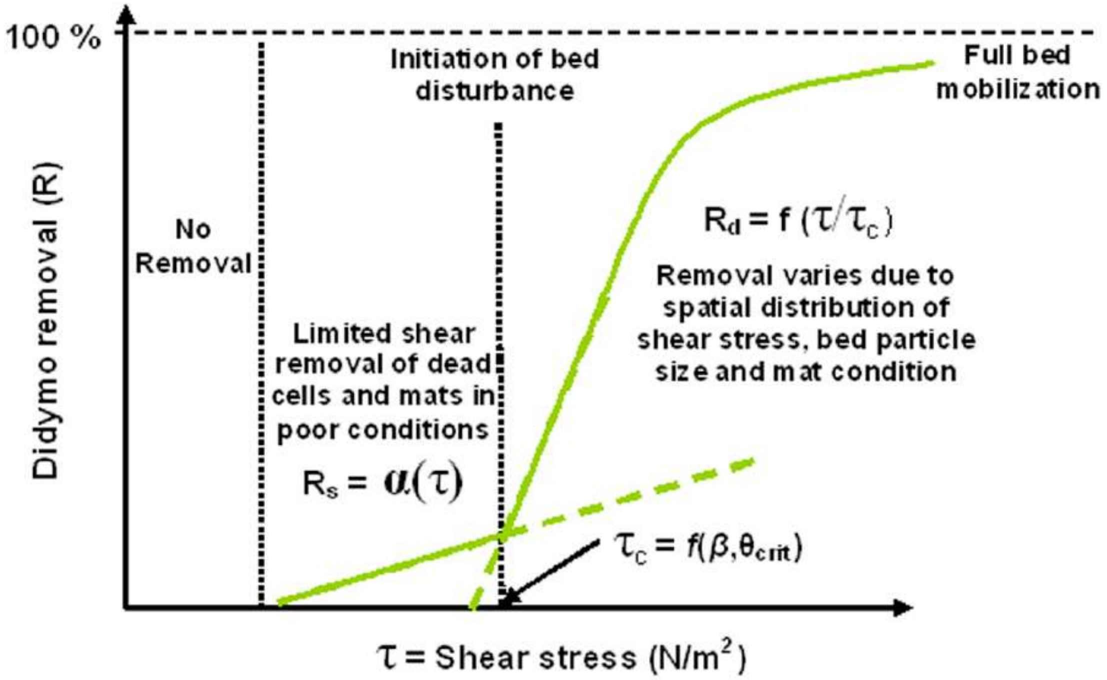

Figure 5.4 **Proposed relationship between average bed shear stress and *D. geminata* removal (*R*) showing that the bulk of biomass removal (R_d) occurs above the critical value for bed disturbance (τ_c), but that below this value there is likely to be some shear removal (R_s), particularly of dead 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.**

The critical disturbance threshold for sediment transport in rivers is a function of both channel slope and bed 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 5.4. 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.

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 preconditioning, i.e., the range of shear stresses to which the mat is typically exposed (Biggs & Thomsen, 1995). The specific shear removal function for *D. geminata* (Rs) is currently unknown. As an initial estimate, we proposed that Rs increasing linearly with shear stress above a critical value (Figure 5.4), 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.

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.

5.6 Colonization and Recovery after Disturbance

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 & Stevenson, 1991). The potential for colonization of the substrate by 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 5.5. 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.

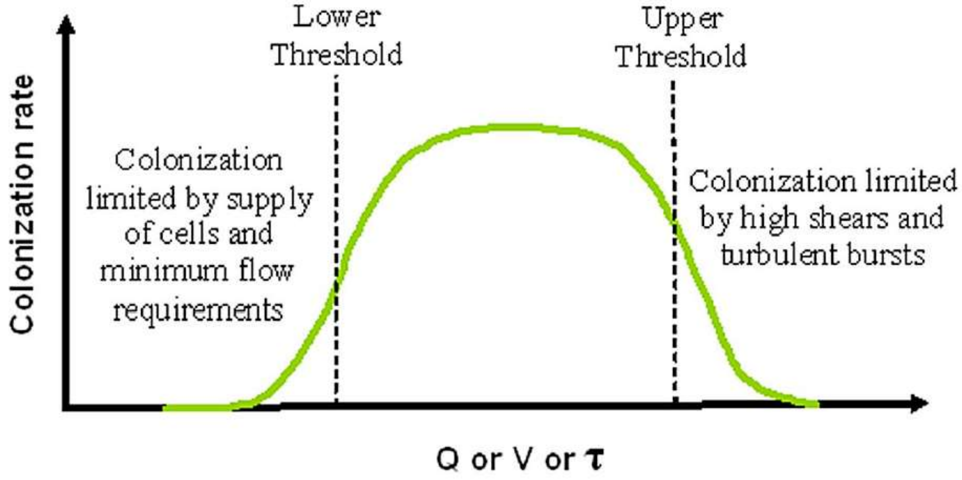

Figure 5.5 **Proposed relationship between the colonization rate and increasing flow (Q), velocity (V), or shears stress (τ)**

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 & 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).

5.7 Distinguishing Mat Growth from Cell Division

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.

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 & 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.

The proposed response of *D. geminata* to increasing nutrient concentrations is shown in Figure 5.6. 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 & 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).

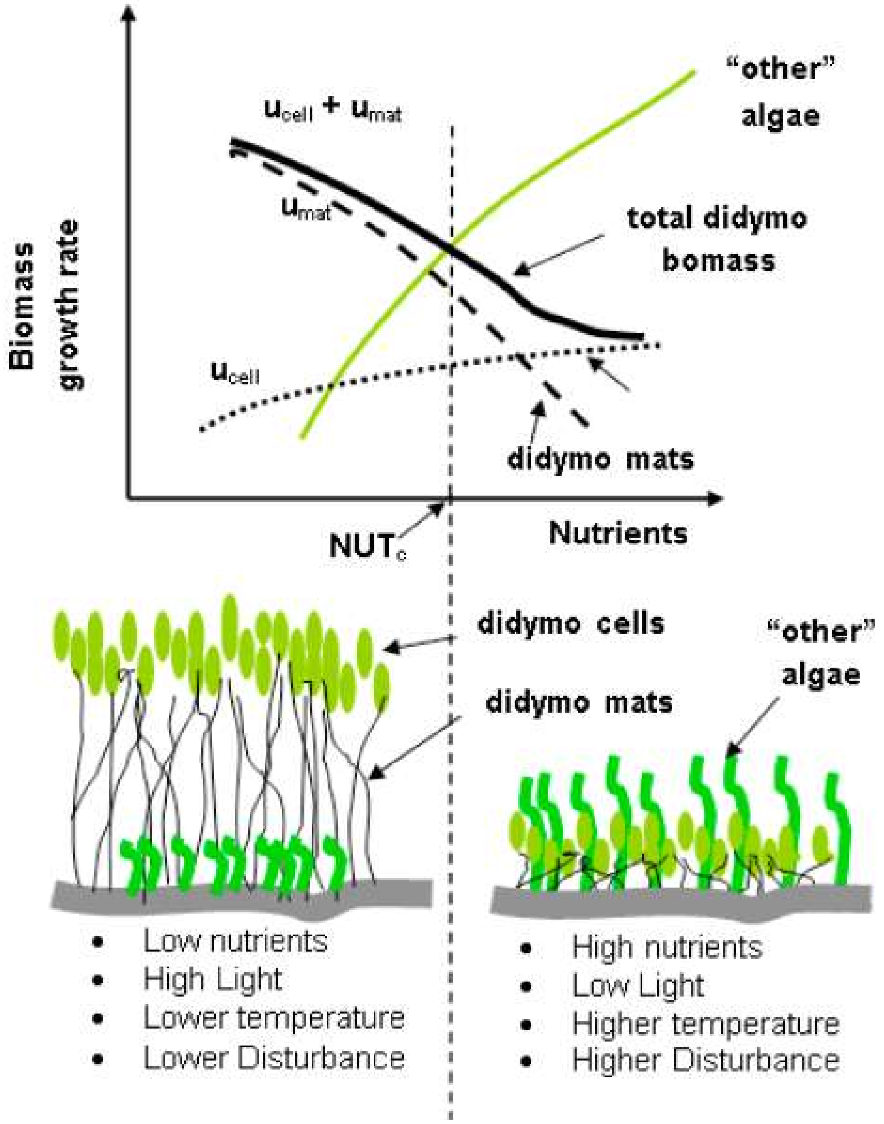

Figure 5.6 **Hypothesized relationship between biomass growth rate (ΔB/Δt) and nutrient concentrations for cells, mats, and total biomass of *D. geminata* compared to other potentially competing benthic algae. The critical nutrient threshold (NUTc), indicated by the dashed line, is the point at which *D. geminata* loses its dominance over competing algae.**

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 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.

5.8 A Preference for High Light Environments

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 & Kilroy, 2011) and stalk length (Kilroy & 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 5.3) by a threshold value of photosynthetically active radiation (PAR) reaching the streambed (PAR > PARc).

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).

5.9 Temperature as a Controlling Variable

Although *D. geminata* cells have been observed in a wide range of average stream temperatures (Spaulding & 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 & 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.

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 5.3 as a threshold value of $T < Tc$. It is however unclear exactly what measure of stream water temperature is significant, what the critical value is, or even whether temperature is a primary control on *D. geminata* growth or just an indicator of other unknown controls.

5.10 Water chemistry and Secondary Nutrients

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).

5.11 Impacts of grazing

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 & 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 & 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 & 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 (Kilroy *et al.*, 2009; Gillis & Chalifour, 2010).

5.12 Summary of the Conceptual Model

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:

1. Translocation by humans is a significant vector for the invasion into new watersheds.
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.
3. Flood events sufficiently large to mobilize the substrate are the primary control on the removal of *D. geminata*.
4. Dense and thick mats alter local hydrodynamic conditions to favor persistence.
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.
6. Key to understanding the didymo paradox of high biomass production under low nutrient conditions is a separation of mat growth from cell growth.
7. The production of longer stalks under lower nutrient conditions, but high light availability is primarily as a result of photosynthetic overproduction.
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.
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.

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.

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 5.1. 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 5.1, although the majority is currently unknown.

5.13 Future Research

Suggestions for research to further develop and determine the key parameters in the proposed conceptual model are given in Table 5.1. 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.

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 5.1 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	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].

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 & Wilcock, 1996) including for the management of nuisance algal blooms (Flinders & 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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CHAPITRE 6

EFFECT OF DISCHARGE AND HABITAT TYPE ON THE OCCURRENCE AND SEVERITY OF *DIDYMOSPHENIA GEMINATA* MATS IN THE RESTIGOUCHE RIVER, EASTERN CANADA

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Abstract

Since 2006, the Restigouche River watershed, eastern Canada, has been affected by nuisance growths of the mat-forming diatom, *Didymosphenia geminata*. In 2010, in view of the potential impacts of this alga on the local Atlantic salmon fishery, we created a volunteer monitoring network to assess *D. geminata* mat severity within the watershed. Over the course of six monitoring summers, more than 1200 observations of *D. geminata* mat severity were reported in 20 sub-watersheds of the Restigouche River basin. Observations were mapped to illustrate the yearly severity of *D. geminata* mats throughout the watershed. Metrics were then extracted from this dataset to assess the spatial and temporal variability of mat severity. At the reach scale, *D. geminata* occurrence was predominantly found in riffles compared to any other river habitat type. At the watershed scale, a two-sample KS-test highlighted a significant effect of maximum spring discharge on mean annual *D. geminata* mat severity, indicating that when maximum spring discharge is high, severity of *D. geminata* mats in the following months is significantly lower. Additionally, maximum spring discharge explained 71% of the variability in annual mat severity. This study contributes to the understanding of mat severity dynamics and illustrates the value of volunteer monitoring networks for studying complex ecosystem dynamics.

6.1 Introduction

In July 2006, unprecedented algal growths were reported in the Matapedia River, a major tributary of Restigouche River, one of the most important Atlantic salmon rivers of the Gaspe Peninsula in eastern Canada. The growths were identified as *Didymosphenia geminata* (Lyngbye) M. Schmidt, a mat-forming diatom frequently associated with the clear and cold waters of pristine rivers. This was the first incidence of this species reported at nuisance levels in eastern North America. *D. geminata* can produce thick growths of dense fibrous stalk material covering the entire streambed surface and persist for several months (Biggs, 1996; Larned *et al.*, 2007; Spaulding & Elwell, 2007) (Figure 6.1). It is therefore not surprising that it has been reported to modify the aquatic food base, alter ecosystem structure and function (Larned *et al.*, 2007; Gillis & Chalifour, 2010) and decrease the aesthetic value of affected rivers (Spaulding & Elwell, 2007; Beville, 2012). Soon after its appearance in 2006, *D. geminata* became conspicuous in many other rivers of the Gaspe Peninsula and New Brunswick, Canada. However, several rivers remained unaffected, raising questions as to why mat formation would occur in some rivers and not others. In their conceptual model for the blooming behavior and persistence of *D. geminata,* Cullis *et al.* (2012) emphasized the role of water chemistry, river morphology and flow thresholds in defining the habitat window of this alga. According to this model, cold, clear and shallow water are required to provide the amount of light necessary for the growth of *D. geminata,* while high flow events generate the critical shear stress and bed material transport causing the removal of the algae. Although the conceptual model is based on numerous field observations, the authors concluded that the validation of its components would require field data offering both good spatial coverage and longer time series observations. In fact, most of the existing studies on the variability of *D. geminata* encompass, on average, a two-year period.

In eastern Canada, although some regional scale observations provided insights on the distributional range of *D. geminata,* presence-absence data were scarce and too infrequent to allow a comprehensive analysis of the factors determining its distribution. In addition, observation methods were not standardized across stakeholders and agencies, therefore limiting comparability of mat severity between watersheds. Thus, a more systematic monitoring program was required. To achieve the collection of a long-term dataset while constrained by limited financial resources, there was therefore a need to create a *D. geminata* monitoring network following a citizen science approach. Several examples have shown the ability of citizen science to gather valuable scientific data while involving citizens in a true collaborative partnership with academia (Chopyak & Levesque, 2002; Crall *et al.*, 2010). Such an approach has, for example, contributed to the early detection and monitoring of emerging nuisance species across local and regional scales (Lodge *et al.*, 2006; Crall *et al.*, 2010).

Figure 6.1 Large growths of *D. geminata* mats in the Duval River, a tributary of the Bonaventure River, Gaspesie, Quebec, Canada

In the case of the Restigouche River, the first objective was therefore to identify habitat types most favorable to the *D. geminata* mat formation and persistence. This was accomplished by collecting a comprehensive dataset describing the longitudinal distribution of river habitat types and *D. geminata* mat occurrence along a 65 km-long section of the Matapedia River in 2007. The second objective was to involve volunteers from several key organizations to generate a long-term dataset from standardized visual monitoring of *D. geminata* describing this alga's spatial and temporal variation throughout the watershed for at least six years, beginning in 2010. Lastly, the final objective was to analyze the dataset generated from the monitoring network to determine the effect of discharge on the inter-annual variability of *D. geminata* mat severity.

6.2 Methods

6.2.1 Study Area

Located in eastern Canada, the Restigouche River drains an interprovincial watershed (Quebec and New Brunswick) of more than 12 000 km^2 and has five major tributaries: the Matapedia River, Patapedia River, Kedgwick River, Little Main River and Upsalquitch River. The study area is unregulated and has a snow-melt dominated hydrological regime. These rivers have had occasional to persistent growth episodes of *D. geminata* since 2006 (Gillis & Chalifour, 2010).

6.2.2 Reach scale mapping of habitat type and *D. geminata* mat occurrence along the Matapedia River

Between August 5th and 28th 2007, during stable low flow conditions, the Matapedia River was surveyed to assess presence-absence of *D. geminata* mats along a 65 km-long section of the river. Along the longitudinal transect, each channel unit was classified into homogeneous mesohabitat types according to bed topography and low water surface flow facies as defined in Frissell *et al.* (1986). Habitat types were categorized in terms of depth, substrate and velocity, as either rapids, runs, pools or riffles (Table 6.1). Within each unit, we assessed substrate composition, channel width and depth as well the occurrence of *D. geminata* mats. Visual surveys of *D. geminata* mat presence-absence were conducted with a viewfinder from a canoe.

Table 6.1 Definitions and features of categorized habitat types. Adapted from Harding *et al.* (2009).

Habitat type	***Depth***	***Flow***	***Surface flow pattern***
Rapid	Shallow to moderate	Swift and strong currents	Surface broken with white water
Riffle	Shallow	Moderate to fast with mixed currents	Surface rippled but unbroken
Pool	Deep	Slow	Smooth
Run	Shallow to moderate	Slow to moderate, uniform	Surface unbroken, smooth

6.2.3 Didymo Monitoring Network (DoMiNo) development and quality control

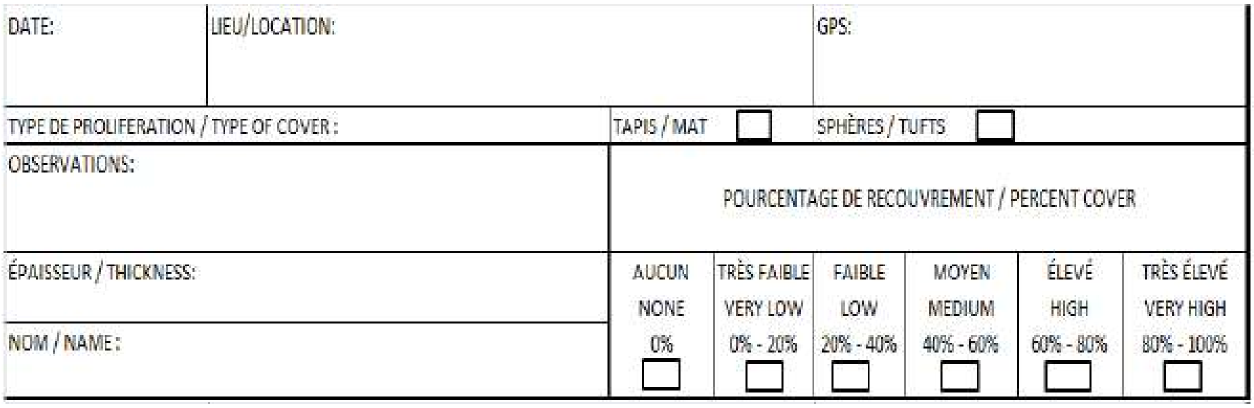
To develop an effective monitoring network, we approached key organizations involved in Atlantic salmon fisheries that were keen to understand how this nuisance alga affected fish habitat and potentially the local economy. Recruitment of these partners (e.g. fishing/hunting outfitters, fishing camps, watershed organizations, canoers, kayakers, anglers and field technicians, see Table 6.2) helped define monitoring site locations. While aiming for a well distributed sampling effort, care was taken to make it possible for volunteers to include data collection in their daily routine. This approach yielded a high participation rate amongst targeted groups and promoted volunteer retention through the duration of the study. Within the Restigouche River watershed, the network currently involves 70 volunteers from 22 different key organizations with an interest in Atlantic salmon conservation.

Table 6.2 Overview of organizations monitoring the occurrence and severity of *D. geminata* mats throughout the Restigouche River watershed

Organization	Type	Nb. trained volunteers	Nb. monitored rivers
Fed. Quebecoise Saumon Atlantique	Anglers	2	6
Matapedia-Restigouche Watershed	River management	4	10+
Restigouche River Watershed Management Council	River management	3	7
Listuguj Rangers	Conservation	2	1
Arpin Canoe Restigouche	Ecotourism	4	5
Nature Aventure	Ecotourism	3	9
ZEC Casault	Outfitter	1	1
CGRMP	Outfitter	12	14
Auberge de la Riviere Matapedia	Outfitter	1	2
Fishing Camps	Private	31	9
Dept. of Fisheries & Oceans	Science	4	20+
Centre Interuniversitaire de la recherche sur le saumon atlantique	Science	3	2

6.2.3.1 DoMiNo Volunteer Booklet

To assist volunteers in the proper collection of data, an English and French educational booklet was developed. First, the text addressed the importance of the monitoring network and reminded volunteers of the importance of this effort towards the advancement of *D. geminata* research. It also provided information on the general biology and ecology of the diatom and described how their efforts would be integrated in research questions and objectives. The data collection protocol was presented into detail to remind participants how observations should be collected. The protocol involved a visual classification of *D. geminata* presence into five different categories of percentage of bed coverage by *D. geminata* in increments of 20%. To limit biased estimates of mat coverage, photographs, representative of each category, were provided in the photo-guide section of the booklet. One representative measurement of mat thickness was then determined with a ruler. Pre-formatted waterproof data sheets (Figure 6.2) were provided to ensure that all relevant information was collected (i.e. name of the observer, date, location, percent cover category, thickness and type of coverage (mats or tufts) and allowed for consistency in data collection among volunteers.



DATE:	LIEU/LOCATION:			GPS:		
TYPE DE PROLIFERATION / TYPE OF COVER :	TAPIS / MAT ☐			SPHÈRES / TUFTS ☐		
OBSERVATIONS:	POURCENTAGE DE RECOUVREMENT / PERCENT COVER					
ÉPAISSEUR / THICKNESS:	AUCUN NONE 0% ☐	TRÈS FAIBLE VERY LOW 0% - 20% ☐	FAIBLE LOW 20% - 40% ☐	MOYEN MEDIUM 40% - 60% ☐	ÉLEVÉ HIGH 60% - 80% ☐	TRÈS ÉLEVÉ VERY HIGH 80% - 100% ☐
NOM / NAME :						

Figure 6.2 Data collection sheet used by the volunteers to monitor *D. geminata* percent cover and mat thickness

6.2.3.2 Training

At the beginning of each monitoring summer, participants of each organization took part in an interactive training session where they were taught how to identify *D. geminata* adequately, how to use the monitoring network booklet and collect data. When possible, volunteers were also accompanied in the field by the authors to conduct live search and identification of *D. geminata*. As recommended by Bonter and Cooper (2012), frequent follow-ups (i.e. communication and field visits) were conducted throughout the sampling period to ensure proper monitoring, data quality and limit inter-operator variability (Kilroy *et al.*, 2013).

6.2.3.3 Data collection

Between 2010 and 2015, volunteers gathered weekly observations of *D. geminata* mat coverage and thickness data with their DoMiNo booklet in their assigned sites between mid-May and late October of each year. Each organization then forwarded the information on a fortnight basis for data quality control and compilation. Thus, data reported by volunteers was frequently validated by field visits and/or by corroborating estimations with supplemental photos. Moreover, all newly reported affected reaches (first positive report for a given watercourse) were visited by the authors. Per year, we visited, on average, 25% of the monitored sites for in-field validation of *D. geminata* percent cover and thickness. All validated observations were geo-referenced. Over the course of six monitoring periods (2010-2015), volunteers gathered 1228 validated observations of *D. geminata* mat severity throughout the Restigouche River.

6.2.4 Data analysis

6.2.4.1 Reach scale occurrence of D. geminata mats

A contingency table of the frequency of occurrence of *D. geminata* mats within each habitat type was developed for the 2007 survey data. Pearson's chi-square test was applied to the frequency data of *D. geminata* mats in relation to habitat type and substrate and used to highlight habitat preferences for mat formation.

6.2.4.2 Mat severity: Standing Crop Index

When each visual observational data was compiled into the regional database, a Standing Crop Index (SCI) value was calculated by multiplying the thickness of the *D. geminata* mat by its percent areal coverage.

This method was initially developed by Kilroy (2006) and enables the production of a standardized metric that can be compared across local, regional, national and international scales (Kilroy & Bothwell, 2012). In this manuscript, we use the Standing Crop Index as a proxy defining *D. geminata* mat severity.

6.2.4.3 Mapping

Standing Crop Index (SCI) observations spanning six monitoring periods (2010-2015) were used to map *D. geminata* inter-annual variability throughout the watershed. For each year, maps were created by interpolating the SCI values, constrained to areas for which observations existed, along the river network. Sites comprising multiple values per monitoring period were averaged to provide mean SCI throughout the monitoring period. Inverse distance weighting (IDW) was applied in a stream-wise direction using a kernel of radius 2.5 km to ensure that interpolated values did not substantially stray outside the limits of the observed data points. Interpolated SCI values were classified according to nuisance periphyton criteria (Kilroy & Wech, 2012), where *green* denotes 'good' status (SCI below 200), *amber* denotes 'alert' status (SCI between 200 and 600) and *red* (SCI above 600) denotes that a management response is required. This method was used as an effective management tool on the Lower Waiau River in New Zealand by characterizing occurrence and severity of *D. geminata* mats (Kilroy & Wech, 2012). Inter-annual variation and spatial distribution of *D. geminata* mat severity was subsequently quantified by calculating the percentage composition of mat coverage in terms of these three severity classes as well as by computing the mean SCI across the entire watershed for each summer monitoring period. Analysis-of-variance (ANOVA) was used to determine whether SCI values varied significantly between streams of different Strahler order.

6.2.4.4 Hydrological data

Annual discharge conditions within the Restigouche watershed were examined to identify potential mechanisms responsible for inter-annual variability in *D. geminata* mat coverage falling into each of the three severity classes (green-yellow-red). Daily discharge data were assembled by combining records from two gauging stations located towards the confluences of the Matapedia and Restigouche sub-basins (Environment Canada ID 01BD009 and 01BJ007 respectively). A series of simple regression analyses (linear, exponential, power) was used to explore correlations between *D. geminata* mat severity and a range of hydrological metrics. These metrics comprised mean, minimum and maximum annual discharge, peak spring discharge (defined as maximum daily discharge between February 1st and May 31st), number of high discharge events (defined as the number of days where discharge exceeded a predefined threshold of 65 m^3s^{-1}) and number of days since flood. If regression analysis indicated the existence of a correlation between *D. geminata* severity and a given hydrological metrics, a two sample Kolmogorov-Smirnov test was used to compare distributions of hydrological parameters and SCI.

6.3 Results

6.3.1 Reach scale variability of *D. geminata* mat occurrence

Frequency of *D. geminata* mat occurrence was determined visually for each habitat type (Figure 6.3) in 2007. Visual presence-absence data showed that the occurrence of mats was dependent on the various habitat types (i.e. rapids, runs, pools and riffles) indicating a strong habitat preference for riffles ($\chi2$ (3, N= 276), $p < 0.05$). Conversely, *D. geminata* presence was not dependent on substrate type within riffles ($\chi2$ (3, N= 123), $p > 0.05$).

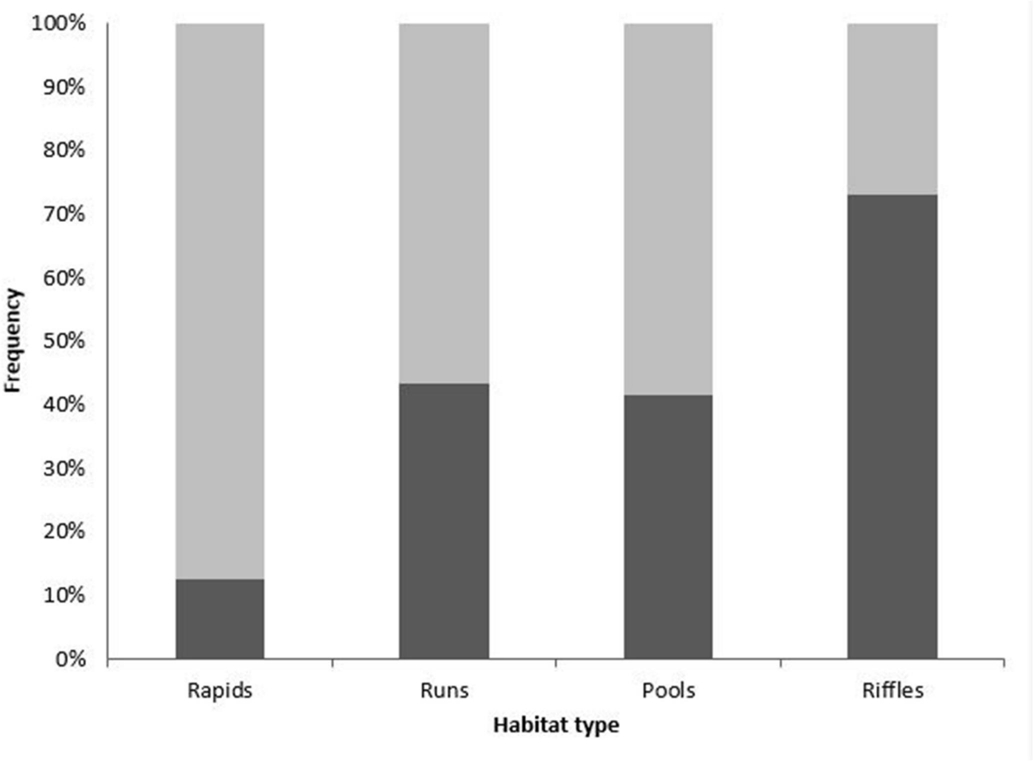


Figure 6.3 **Frequency of *D. geminata* mat presence (dark grey) and absence (light grey) in various habitat types of the Matapedia River**

6.3.2 Inter-annual variability of *D. geminata mat severity*

Data collated between 2010 and 2015 was analyzed and severity maps were created to highlight the yearly spatial variability of *D. geminata* mat severity throughout the Restigouche River watershed (Figure 6.4). Table 6.3 presents the yearly proportion of *D. geminata* mat severity per class. *D. geminata* mat severity was highly spatially variable between monitoring periods. *D. geminata* mats were most severe in 2013 (14.7% of sites under red status). Conversely, *D. geminata* mats were less severe in 2010, 2011, 2014 and 2015, where the percentage of sites under green status was the highest throughout the time series. This trend was observed throughout the watershed across all monitored reaches (Strahler's stream order varying from 4 to 8). One-way analysis of variance (ANOVA) showed that mean SCI values did not vary significantly between stream order.

Table 6.1 Proportion of *D. geminata* mat severity comprising each class per monitoring period in relation to maximum spring discharge

	Percent proportion of SCI levels					
	2010	**2011**	**2012**	**2013**	**2014**	**2015**
Low (<200)	80,1	81,9	65,6	66,0	84,3	89,8
Medium (200 - 600)	15,5	9,9	25,9	19,3	8,8	4,1
High (>600)	4,4	8,2	8,5	14,7	7,0	6,0
Max spring discharge (m^3s^{-1})	1718,8	2452,1	1556,2	1165,1	2553,8	2314,5

Of the various hydrological metrics, maximum spring discharge was the only one that exhibited a significant correlation ($p < 0.05$) with SCI (i.e. *D. geminata* mat severity) under any of our regression analyses (linear, exponential, power). Using a power regression model (Figure 6.5), maximum spring discharge (Q_{max}) explained 71% of the observed variability in SCI ($R^2 = 0.71$, $p < 0.05$). Furthermore, the distributions of mean SCI and maximum spring discharge differed significantly (two-sample KS test: $p < 0.05$) indicating that when maximum spring discharge is high, severity of *D. geminata* mats in the following months will be significantly lower.

6.3.3 Data quality

Over the course of six monitoring periods, less than 2% of the data needed to be corrected due to over or underestimation of *D. geminata* mat severity following field visits and/or photo validation. Furthermore, *D. geminata* was misidentified on only three occasions where another stalk-forming diatom, i.e., *Cymbella sp.* was mistaken for *D. geminata.*

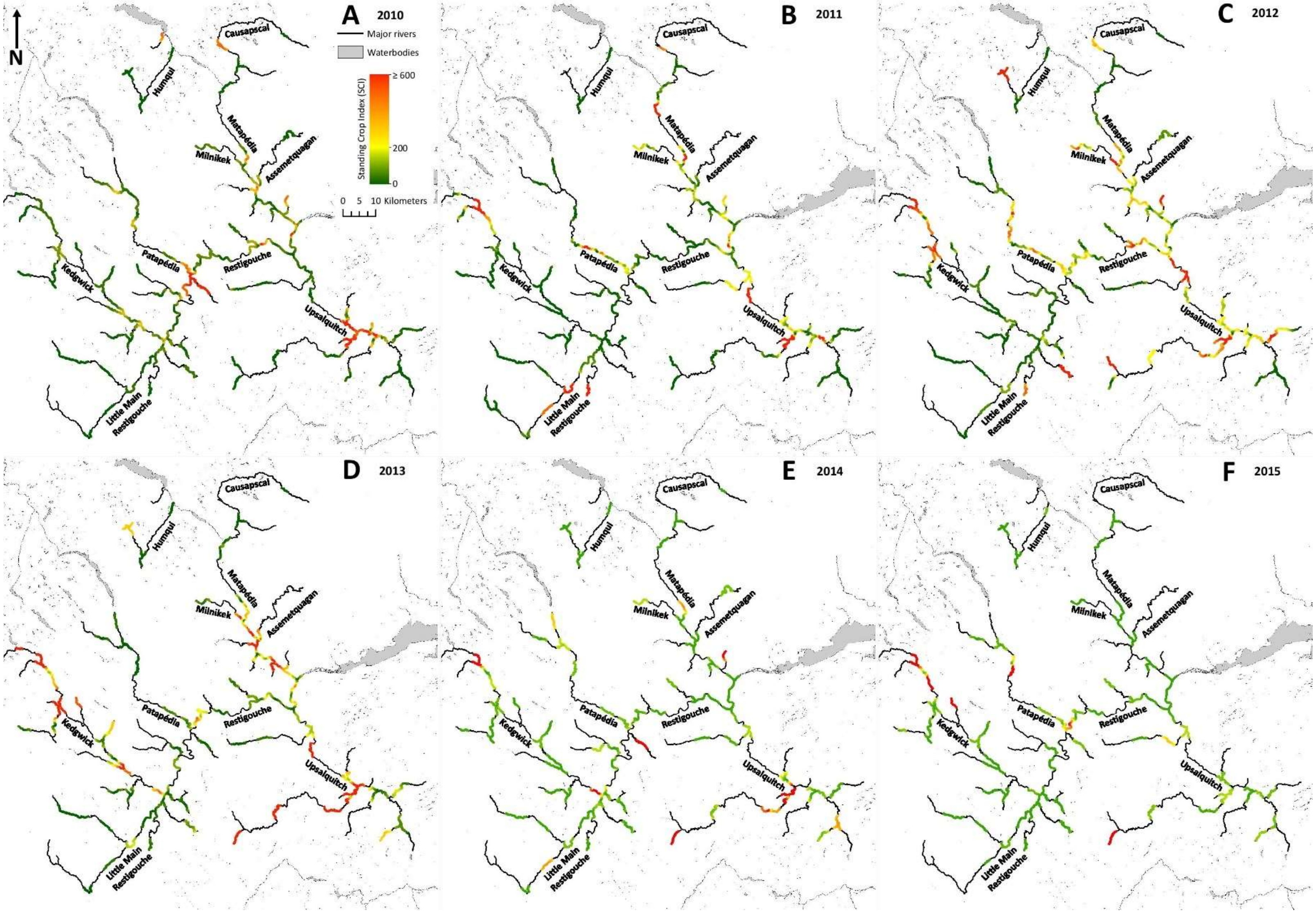


Figure 6.4 Maps of interpolated *D. geminata* mat severity throughout six monitoring periods between 2010 (A) and 2015 (F). Severity scale is presented in map A and color classification is based on Kilroy and Wech (2012); Table 6.3.

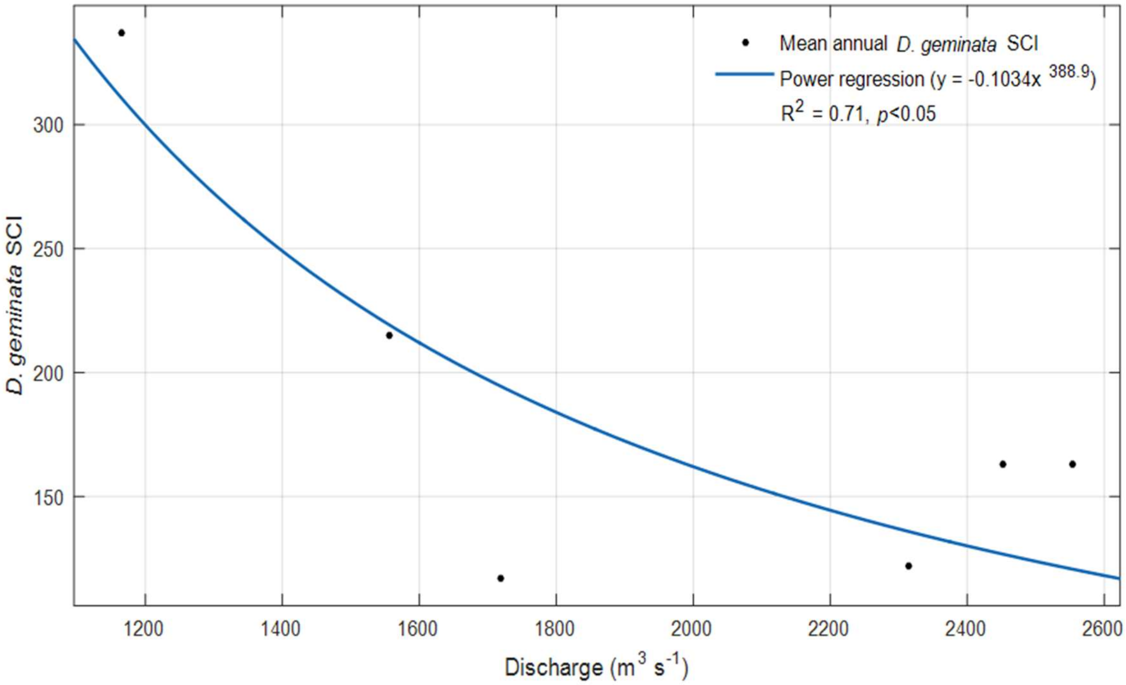


Figure 6.5 **Power regression model of mean annual *D. geminata* SCI in relation to maximum spring discharge (m^3s^{-1})**

6.4 Discussion

In this study, the creation of a didymo monitoring network allowed for the development of a comprehensive dataset describing the spatial and temporal distribution of *D. geminata* in the Restigouche River watershed between 2010 and 2015. The time and effort spent training volunteers resulted in an extensive dataset of reliable observations that could not have been obtained otherwise through a conventional monitoring program, which clearly demonstrates that citizen science can help further the understanding of this nuisance species.

6.4.1 Factors driving *D. geminata* mat occurrence and severity

At the reach scale, our results indicate that the spatial variability in *D. geminata* mat coverage was explained by habitat characteristics. *D. geminata* mats were occasionally found in runs and pools, but were most prevalent in riffles. They were however almost completely absent from rapids. Rapids may render unsuitable conditions due to high shear stress and higher frequency of bed load transport causing mat scouring whereas light availability is limited in deeper pools. This result supports previous observations that geomorphological units define physical habitat suitability for mat colonization and growth (Miller *et al.*, 2009; Cullis *et al.*, 2015). Runs and riffles offer optimal conditions for *D. geminata* colonization, mat development and persistence due to their shallow depths, high light availability and stable substrate between high discharge events.

At the watershed scale, analysis of the correlation between the mean annual SCI against multiple hydrological metrics showed that maximum spring discharge best explained inter-annual variability in SCI. As a corollary, high maximum spring discharge was associated with a lower proportion of "red" or "orange" status for 2011, 2014 and 2015. For example, 2011 was characterized as a "wet" year and *D. geminata* was found to be limited within the basin. In comparison, 2010, 2012 and 2013 were dryer years in eastern Canada with fewer high-flow events that may have limited *D. geminata* growth and mat establishment. Our findings are in accordance with Richardson *et al.* (2014) who found that inter-annual variability of the hydrological regime and higher peak flows limited *D. geminata* density. In our study, maximum spring discharge was the only hydrological factor to have a significant effect on *D. geminata* mat severity. Conversely, in New Zealand, Kilroy and Wech (2012) found that the number and duration of floods above 65 m^3s^{-1} were significantly correlated with the percentage of time that surveys yielded a green status due to reach-scale scouring. They also showed that the number of days since a flood occurred best explained the amount of time under red status. Recent work by George and Baldigo (2015) found that the frequency of high-flow events significantly decreased stalk biomass.

6.4.2 Data reliability and limitations

The quality of data collected by citizen science initiatives is often criticized. However, good quality data can be ensured by proper sampling design, standardized methods and appropriate training (Yoccoz *et al.,* 2003; Delaney *et al.,* 2007; Schmeller *et al.,* 2009). Kilroy *et al.* (2013) found that assessments of visual periphyton surveys by multiple participants was not a challenging issue if given proper training. A review by Crall *et al.* (2010) also highlighted that appropriate training can provide ample scientific skills for neophyte volunteers to collect required data. As in Dickinson *et al.* (2012), the availability of an educational tool (here the monitoring network booklet) promoted and facilitated the collection of appropriate data while maintaining awareness and reminding users of the importance and relevance of their efforts. Quality control of citizen science data is however a necessary step to validate data consistency and reliability (Bonter & Cooper, 2012).

Citizen science datasets are defined by sampling efforts and by the spatial distribution of monitored sites. Thus, resulting distribution patterns are substantiated by the fact that "absence of evidence is not evidence of absence" (Altman & Bland, 1995), and suggest a probable underestimation of the documented phenomenon. It is therefore considered that the visual monitoring efforts carried out by volunteers do not discount watercourses of absolute *D. geminata* presence. Nevertheless, this effort offers good insights on the broad scale occurrence of *D. geminata* across landscapes and the authors are confident that the data obtained ensured an efficient monitoring of *D. geminata* mats. In parallel, this type of extensive monitoring data can help define regional trends in occurrence and severity by comparing existing ancillary physical and chemical data of affected and non-affected reaches.

6.5 Conclusion

The Didymo Monitoring Network was the first network to be developed to monitor the occurrence and severity of *D. geminata* mats. Following this initiative, other organizations are now effectively monitoring *D. geminata* by training and involving volunteers (e.g. The New Hampshire Rivers Council's *River Runners*; the Three Rivers Community College's *Citizen's River Monitoring Program*; the Trout Unlimited *Discovering Didymo Distribution* using the iNaturalist app piloted by the University of Calgary and the University of North Carolina). These project schemes offer potential for partnership and future collaborative efforts will be pursued to enhance our current liked-minded projects across landscapes, state and international boundaries. Yielding a higher standardized sampling effort at greater geographical scales will contribute to the production of a robust dataset enabling ecological modelling of *D. geminata*. Cell vouchers may also be useful in monitoring programs towards increasing quality control and validation of recorded observation data by microscopic identification of cells.

Mapping the severity and distribution of nuisance growths throughout the Restigouche River watershed helped managers and local stakeholders comprehend factors explaining the observed yearly variability. Although hydrological metrics alone cannot define *D. geminata'*s habitat window (Cullis *et al.,* 2012) nor entirely account for observed seasonality and yearly variability (Kirkwood *et al.,* 2007; Kilroy & Wech, 2012), this study highlights trends in inter-annual SCI variability driven by the hydrological regime. A more comprehensive look at *D. geminata* seasonality is needed to highlight the importance of hydrological metrics driving site-specific changes in SCI values. Furthermore, an assessment of the relative importance of other intrinsically related variables to discharge such as temperature and light availability is needed to better define yearly and seasonal trends as well as defining *D. geminata'*s habitat window for colonization, growth and persistence of nuisance growths in eastern Canada. Future research efforts should focus on developing tools for assessing the severity of *D. geminata* nuisance growths by incorporating the timing, duration and proportion of affected vs. non-affected habitats. This biomass assessment may then be incorporated in *D. geminata* ecosystem impact studies.

Acknowledgements

This project would not have been a success without the participation of many volunteers and stakeholders wary of Atlantic salmon conservation and local economy. Thank you for being curious and devoted. This effort has been aided by financial support provided by Mr Gaston Lepage through his donation to the Fondation de l'Université du Québec (FUQ). Additional funding was provided by the Atlantic Salmon Conservation Foundation (ASCF) and the New-Brunswick Wildlife Trust Fund (NBWTF). Carole-Anne Gillis was funded by NSERC-FRQNT BMP-Innovation grant through collaboration and support by the Matapedia-Restigouche Watershed Organization. Thanks to the Conseil de l'eau Gaspésie-Sud and the Restigouche River Watershed Management Council for supplemental support. Many thanks to Anne Provencher St-Pierre for her support during the creation of this monitoring network, to Daniel Caissie for commenting an earlier version of the manuscript and to Jordane Clermont and Danielle Frechette for their support with the dataset and analysis.

CHAPITRE 7

WATER CHEMISTRY DRIVES REGIONAL SCALE DISTRIBUTION OF *DIDYMOSPHENIA GEMINATA* IN QUEBEC RIVERS: A CONTRIBUTION TO THE DIDYMO CONCEPTUAL MODEL

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Version à être soumise pour publication

Abstract

Didymosphenia geminata is a stalk-forming diatom that has recently been emerging in many freshwater ecosystems around the globe where it had not been reported previously. In eastern Canada, observations of nuisance mats of this alga were first reported in 2006 in the Matapedia River. This Atlantic salmon fishing river has several characteristics shown to favor the ability of *D. geminata* to form thick, extensive benthic mats, such as stable flows, oligotrophic nutrient conditions and stable substrate. Since this first report, *D. geminata* cells and visual mats have also been reported in 25 other catchments of Gaspésie and northern New Brunswick rivers. All affected watersheds share favorable characteristics for *D. geminata* growth as depicted in the Didymo Conceptual Model (Cullis *et al.*, 2012). However, the diatom has not been reported in the nearby North shore region, despite their similar low nutrient conditions. Water chemistry data were compared between the two regions. Comparison between the North and South shore regions allowed the identification of key environmental parameters for *D. geminata* growth, with differences primarily due to geology-driven water chemistry. Rivers of the South shore where *D. geminata* is present displayed a high alkalinity (above 60 mg/L) and corresponding higher pH (above 7.5) than rivers on the North shore. Also, rivers supporting *D. geminata* showed lower concentrations of color-causing compounds, such as organic carbon, and clearer water, which supports other research findings showing that high light levels promote stalk production. Increased knowledge in this species' biogeography and scale-dependent water chemistry thresholds are key towards validating and improving the Didymo Conceptual Model.

Keywords: *D. geminata,* mat-forming diatom, water chemistry, geology, nuisance alga, biogeography

7.1 Introduction

Under oligotrophic conditions, the mat-forming diatom *Didymosphenia geminata* (Lyngbye) M. Schmidt can produce excessive amounts of stalk material resulting in thick and extensive fibrous mats covering the riverbed. Native to North America and northern Europe (Patrick & Reimer, 1975), *D. geminata* (a.k.a didymo) growths are of international concern due to its increased prevalence in lotic ecosystems both within and outside of its historical distribution (Spaulding & Elwell, 2007; Blanco & Ector, 2009). *D. geminata* impacts ecosystem function through food web interactions (Campbell, 2005; Shearer *et al.*, 2007; Kilroy *et al.*, 2009; Gillis & Chalifour, 2010) and affects the angling industry and local economies through decreased aesthetic value of streams (Beville *et al.*, 2012). Hence, understanding factors controlling local and regional distribution, such as water chemistry, is key towards effectively managing this nuisance alga (Cullis *et al.*, 2012; Elwell *et al.*, 2014).

Water chemistry is fundamental in defining the distribution of freshwater benthic diatoms (Patrick & Reimer, 1975). Water chemistry in rivers is influenced by catchment geology as well as by land use (Whitton, 1975; Rice & Greenwood, 2001). The Didymo Conceptual Model highlighted that water chemistry parameters were key controlling factors for cellular presence and mat presence which defined the habitat window for this alga (Cullis *et al.*, 2012). In response to an apparent increase in *D. geminata* proliferation worldwide, the majority of earlier studies and literature reviews focused on describing this alga's ecological requirements in an attempt to predict potential local and international distribution (Kilroy *et al.*, 2004; Spaulding & Elwell, 2007; Blanco & Ector, 2009; Kumar *et al.*, 2009). Most studies, however, thrived to identify correlations between water chemistry and *D. geminata* distribution (Kilroy *et al.*, 2005; Kilroy *et al.*, 2006; Kilroy *et al.*, 2007; Spaulding & Elwell, 2007; McLaughlin, 2009b; Montecino *et al.*, 2016). Several of these studies suggest that at a regional scale, the presence of *D. geminata* is associated with low water temperatures and high base flow index (Kumar *et al.*, 2009; Montecino *et al.*, 2016), flood severity (Richardson *et al.*, 2014) and high light availability (James *et al.*, 2014). Inherently, low nutrient concentrations have typically defined regional distribution of *D. geminata* nuisance growths worldwide (Cullis *et al.*, 2012; Bothwell *et al.*, 2014). Cullis *et al.* (2015) have suggested that *D. geminata* has been able to capitalize on the observed anthropogenic increases in nitrogen deposition in high alpine lakes and streams due to its ability to grow under conditions of low phosphorus concentration. These parameters rather define the severity and seasonality of *D. geminata*, whereas other water chemistry thresholds may limit and define the biogeographical range of this species across landscapes (Cullis *et al.*, 2012). In fact, recent work lead by Rost *et al.* (2011) and Kuhajek *et al.* (2014) have shown that many other chemical variables play an important role in defining the habitat window for cellular presence of didymo.

Biogeography of this alga in eastern North America is still limited. In Eastern Canada, the first official report of *D. geminata* nuisance growths was located on the Matapedia River in July 2006. This Atlantic salmon fishing river has several characteristics shown to favor this diatom's ability to form benthic mats including stable flows, low nutrient waters, high light intensities and stable substrate (Gillis & Chalifour, 2010). Since this first observation, many other catchments in the region now have occasional to consistent growth episodes, notably most of the surrounding watersheds on the Gaspe Peninsula (South shore) as well as in northern New Brunswick (Gillis, unpublished data). In comparison, *D. geminata* has not been reported in North shore region rivers although they show hydrological conditions and low nutrient concentrations that should favor its growth. Early ecological niche models and resulting potential distribution map developed by McNyset and Julius (2006) also showed that rivers in both regions may be suitable habitat for *D. geminata* due to this alga's wide range of physical and chemical tolerances (Duncan, 2006; Spaulding & Elwell, 2007). Montecino *et al.* (2016) recently tested spread rates and distribution of *D. geminata* in Chile. They established that once *D. geminata* has been found in a given geographical region, most suitable habitats were colonized within a 5 years period; assuming biogeographic equilibrium had been reached. They also concluded that rivers not presently invaded might be unsuitable and remain free of *D. geminata* in the future. Since nuisance levels of *D. geminata* were first reported in Quebec almost ten years ago, it is fair to suggest that such biogeographic equilibrium has probably now been reached.

Geology-driven water chemistry has been shown to be one of the most important factors defining periphyton community composition (Biggs *et al.*, 1990). Because the South shore where *D. geminata* nuisance growths have been reported has predominately sedimentary bedrock geology while the North shore is a mixture of metamorphic and intrusive rocks, it is reasonable to presume that the two locations may have contrasting water chemistry which could affect the establishment of didymo. Regional scale distribution may therefore be defined by water chemistry thresholds as requirements for successful colonization, growth and persistence of *D. geminata* (Whitton *et al.*, 2009; Cullis *et al.*, 2012; Bothwell *et al.*, 2014). The objective of this study was to investigate how water chemistry parameters and geology, at the regional scale, may define the habitat window for *D. geminata* occurrence and distribution in Quebec rivers.

7.2 Material and Methods

7.2.1 Study Area

The Gaspé Peninsula and lower St. Lawrence regions are located on the southern shore of the St. Lawrence River (Québec, Canada) (Figure 7.1) and are part of the northern Appalachian mountain range. In comparison, the North shore region is located north of the St. Lawrence River and east of the Saguenay region, within the Canadian Shield physiographic region (Figure 7.1). Rivers from the South and North shore regions are both snow-melt dominated with similar hydrological regimes (Rousselle *et al.*, 1990).

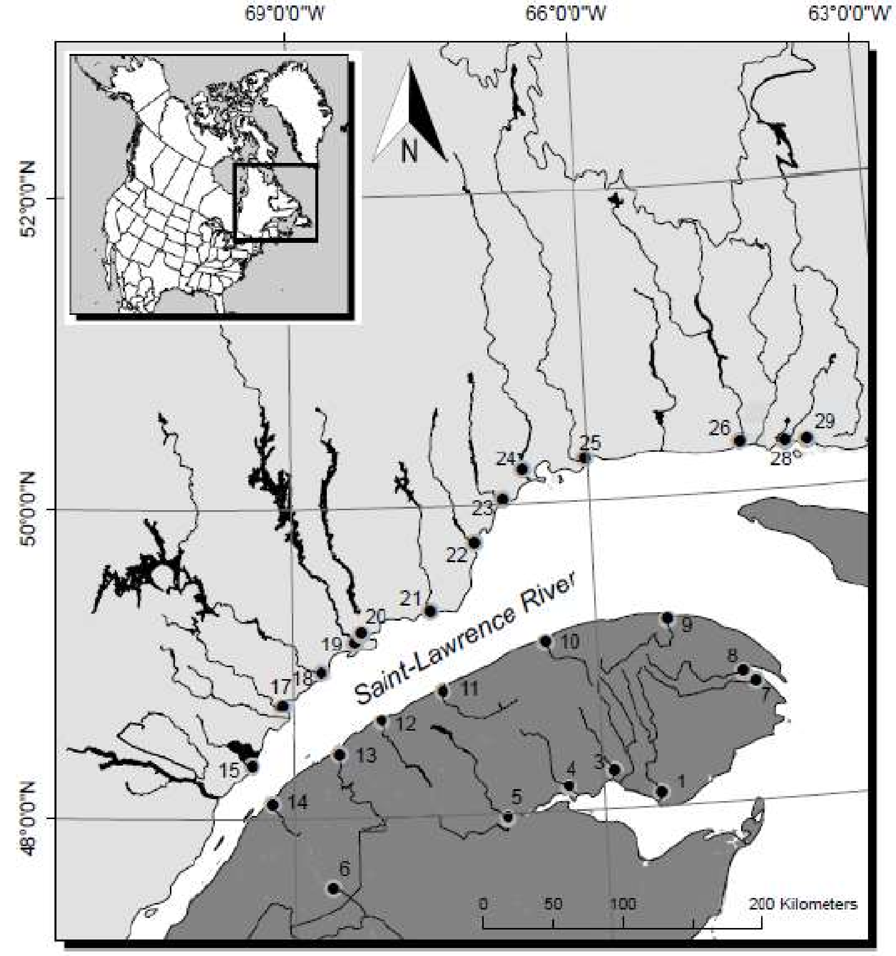

Figure 7.1 **Water chemistry sampling sites of the South shore (dark grey) and North shore (light gray) in Québec, Eastern Canada. For site codes, refer to Table 7.1.**

7.2.2 Presence-absence of *D. geminata*

The current known distribution of *D. geminata* in Quebec is based on detection surveys (microscopy analyses of drift samples) carried out by the Ministère du Développement Durable, de l'Environnement et de la Lutte aux Changements Climatiques (MDDELCC) between 2006 and 2009 (MDDEP, 2009) and on standardized visual reports of periphyton gathered by trained participants of the *D. geminata* monitoring Network (DoMiNo) established in 2010 (See Chapter 6). In recent years, *D. geminata* was exclusively reported in rivers from the Gaspé Peninsula and lower St. Lawrence regions (both referred to as South shore from hereon) and, to this day, there are no reports of its presence in the rivers of the North shore region. This data set describing the spatial distribution of *D. geminata* in the province was used to pool sampling sites in two groups: those in rivers with and without presence reports.

7.2.3 Statistical Analysis

Based on this presence-absence data set of *D. geminata* in rivers of both physiographic regions and available water chemistry datasets, twenty-six rivers were selected from the provincial governmental agency MDDELCC's - Banque de données sur la Qualité du Milieu Aquatique (BQMA) water quality database (Table 7.1). Water chemistry data for each parameter was averaged and standard deviations calculated for rivers with and without a recorded presence, ignoring any parameter with fewer than 10 water chemistry samples within a region and excluding values below detection limits. Of the twenty-six rivers selected, 10 rivers had a recorded presence and 16 had no recorded presence of *D. geminata* (Table 7.1). In Quebec, the existing water chemistry data is mostly pre-2006 prior to *D. geminata* onset and where water chemistry data are concurrent with *D. geminata* presence for 4 of the 26 sites.

Table 7.1 **Water chemistry sampling sites for the South Shore (grey) and North Shore (white) in Quebec and presence (1) and absence (0) of *Didymosphenia geminata***

Site Code[1]	Map Code	River	Years of WC sampling	*D. geminata* presence	Year detected	Reference	Detection method
1080001	1	Bonaventure	1980 -2010	1	2006	MDDEP, 2009	Wisconsin net
1100002	3	Grande Cascapedia	1980-1986	1	2006	MDDEP, 2009	Wisconsin net
1120001	4	Nouvelle	1980-1997	1	2006	MDDEP, 2009	Wisconsin net
1150003	5	Matapedia	1980-1996	1	2006	MDDEP, 2009	Wisconsin net
1170001	6	Madawaska	1980-2010	0	2009	MDDEP, 2009	Wisconsin net
2030001	7	St-Jean	1980-1986	1	2009	DoMiNo, unpub.	Visual Report
2040001	8	York	1980-1997	1	2008	MDDEP, 2009	Wisconsin net
2080001	9	Madeleine	1984-1986	1	2008	MDDEP, 2009	Wisconsin net
2140002	10	Sainte-Anne	1980-1986	1	2006	MDDEP, 2009	Wisconsin net
2160002	11	Matane	1980-1997	1	2006	MDDEP, 2009	Wisconsin net
2190001	12	Mitis	1980-1997	1	2009	DoMiNo, unpub.	Visual Report
2200001	13	Rimouski	1980-1986 2001-2010	0	-	MDDEP, 2009	Wisconsin net
2230001	14	Trois Pistoles	1980-1986	0	-	MDDEP, 2009	Wisconsin net
7020002	15	Des Escoumins	1980-2010	0	-	DoMiNo, unpub.	Visual Report
7050001	17	Du Sault	1980-1986	0	-	DoMiNo, unpub.	Visual Report
7070001	18	Betsiamites	1980-1986	0	-	DoMiNo, unpub.	Visual Report
7100001	19	Aux Outardes	1980-1996	0	-	DoMiNo, unpub.	Visual Report
7110001	20	Manicouagan	1980-1996	0	-	DoMiNo, unpub.	Visual Report
7140001	21	Godbout	1980-1986	0	-	DoMiNo, unpub.	Visual Report
7170001	22	Pentecote	1980-1986	0	-	DoMiNo, unpub.	Visual Report
7190001	23	Aux Rochers	1980-1986	0	-	DoMiNo, unpub.	Visual Report
7210001	24	Sainte-Marguerite	1980-1986	0	-	DoMiNo, unpub.	Visual Report
7230003	25	Moisie	1980-1996	0	-	Hamilton, pers. comm.	Rock scrapings
7350003	26	Magpie	1981-1985	0	-	DoMiNo, unpub.	Visual Report
7370001	28	Mingan	1981-1985	0	-	DoMiNo, unpub.	Visual Report
7380003	29	Romaine	1980-1986	0	-	DoMiNo, unpub.	Visual Report

[1] Site codes as referenced by the MDDELCC BQMA water chemistry database

All subsequent analyses were conducted in R (R Core Team, 2015). Thirty water chemistry parameters were retained. To limit the overemphasis of the contribution of concomitant variables, autocorrelation of all water chemistry parameters was conducted. Eight of the thirty water chemistry parameters were therefore retained as potential non-redundant explanatory variables for a Principal Component Analysis (PCA). The first two principal components were then compared between the two regions using a logistical regression model for both PC1 and PC2 loadings using the Generalized Linear Model (GLM) function to create binary probabilities of specific water chemistry parameters to be associated with *D. geminata* presence or absence.

7.3 Results

Mean values and standard deviations of the 30 water chemistry parameters are presented in Table 7.2. The PCA analysis identified water chemistry drivers and potential controls for *D. geminata* presence and absence (Figure 7.2). The first two components explain more than 82% of the total variance of the data, with 67.47% explained by PC1 and the second principal component accounting for 15.37%. Given the relative loadings of each river on the first two components, rivers from both physiographic regions are separated on PC1 with rivers from the South shore all showing negative loadings and rivers from the North shore all showing positive loadings. Rivers where *D. geminata* is present show common positive relationships with calcium, inorganic carbon, total nitrogen, conductivity, sulfate and sodium. These rivers also show negative relationships with iron and dissolved organic carbon. Of the rivers without a recorded presence of the alga, three of them show a negative relationship on PC1, although the value of their loadings is lower than rivers where *D. geminata* is present. These three rivers are located on the South Shore of the Saint-Lawrence west of the Gaspe Peninsula where nutrient conditions may be contrasting. Loadings of each principal component are presented in Table 7.3.

Table 7.2 MDDEP-BQMA Water chemistry data from 26 Québec rivers where *D. geminata* is present (10 rivers) or absent (16 rivers)

Parameter	Detection level	Units	*D. geminata* present Mean ± SD	*D. geminata* absent Mean ± SD
Alkalinity	0	mg/L	80.3 ± 15.6	13.65 ± 20.6
Ammonia	0.02	mg/L	0.023 ± 0.007	0.022 ± 0.008
Calcium	0.1	mg/L	28.1 ± 5.8	5.3 ± 7.3
Chlorides	0.1	mg/L	3.3 ± 1.5	2.1 ± 1.5
Conductivity	1	µS/cm	175.5 ± 29.3	44.3 ± 46.1
Cyanide	0.003	mg/L	0.0018 ± 0.0008	0.0017 ± 0.0004
Dissolved Fluorides	0.04	mg/L	0.04 ± 0.01	0.04 ± 0.01
Dissolved Iron	0.2	mg/L	0.07 ± 0.06	0.18 ± 0.11
Dissolved Organic Carbon	0.2	mg/L	2.0 ± 1.2	4.9 ± 0.7
Dissolved Oxygen	0	mg/L	12.3 ± 0.2	12.4 ± 0.6
Extractable Manganese	0.01	mg/L	0.014 ± 0.005	0.018 ± 0.01
Hardness	0.4	mg/L	86.7 ± 16.3	17.7 ± 21.25
Inorganic Carbon	0.5	mg/L	18.9 ± 3.5	3.3 ± 4.9
Magnesium	0.1	mg/L	3.9 ± 0.8	0.9 ± 08
Manganese	0.01	mg/L	0.011 ± 0.006	0.009 ±0.004
Nitrate and Nitrite	0.2	mg/L	0.21 ± 0.03	0.09 ± 0.06
pH	3.4	-	7.9 ± 0.1	6.5 ± 0.6
Potassium	0.1	mg/L	0.5 ± 0.2	0.5 ± 0.2
Silica	0.1	mg/L	4 ± 1	4 ± 1
Sodium	0.1	mg/L	2.7 ± 1.2	1.7 ± 1.1
Sulfate	0.5	mg/L	8.3 ± 6.9	2.9 ± 2.3
Tannins and Lignins	0.1	mg/L	0.3 ± 0.1	1.1 ± 0.3
Total Carbon	1	mg/L	24.4 ± 3.4	12.4 ± 5.3
Total Dissolved Phosphorus	0.006	mg/L	0.009 ± 0.001	0.013 ± 0.010
Total Nitrogen	0.2	mg/L	0.5 ± 0.1	0.2 ± 0.1
Total Particulate Phosphorus	0.001	mg/L	0.011 ± 0.003	0.017 ± 0.011
Total Phosphorus	0.01	mg/L	0.021 ± 0.003	0.029 ± 0.017
Total Suspended Solids	0.2	mg/L	10 ± 4	9 ± 11
True Color	1	UCV	6.8 ± 4	28 ± 9
Turbidity	0.1	UNT	4 ± 2	3 ± 4

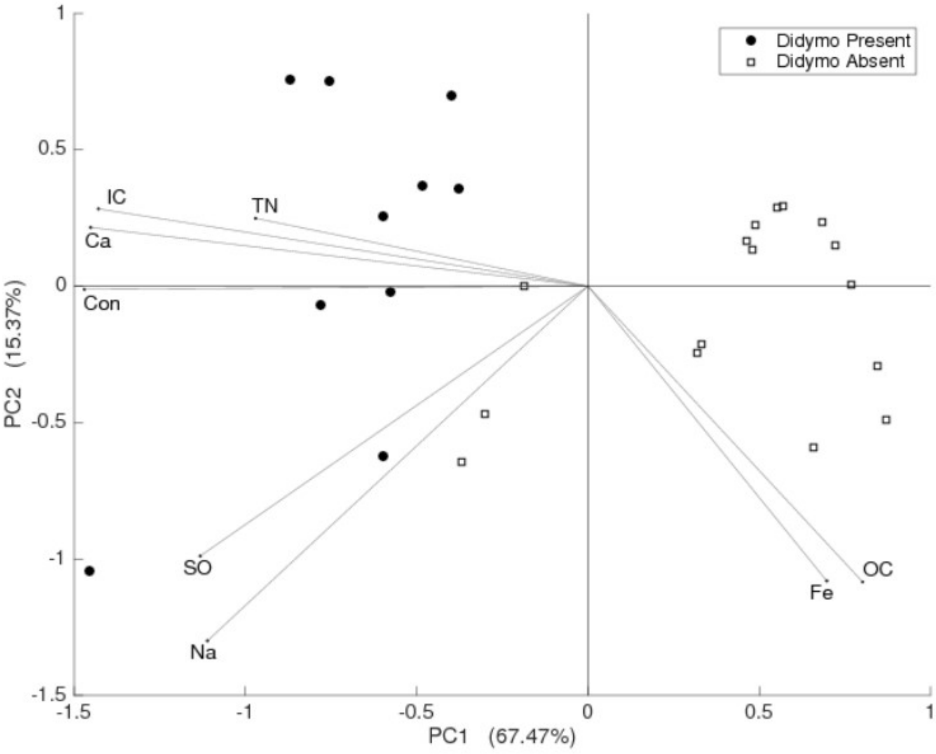

Figure 7.2 Principal component analysis (PCA) of selected water chemistry data. Open squares indicate rivers in which *D. geminata* is absent and closed circles where it is present. Water chemistry labels are as follows: Ca = calcium, CON = conductivity, Fe = iron, IC = inorganic carbon, OC = organic carbon, SO = sulfate, Na = Sodium, TN = total nitrogen.

Table 7.3 Loadings of water chemistry variables incorporated in the PCA and associated eigenvalues and cumulative variance of the first two principal components (Figure 7.2).

Parameter	PC 1	PC 2
Calcium	-1.45	0.28
Dissolved Iron	0.70	-1.08
Dissolved Organic Carbon	0.80	-1.08
Inorganic Carbon	-1.43	0.28
Sulfate	-1.13	-0.99
Total Nitrogen	-0.97	0.25
Eigenvalue	**4.75**	**1.08**
Cumulative variance (%)	**67.47**	**15.37**

The combined fitted logistic regression model of PC1 and PC2 did not converge and defined PC1 as the component explaining the greatest variability between stream sets while the role of PC2 was not significant. The logistic regression of PC1 converged (Fisher scoring = 25; AIC = 4) and yielded a binary probability of a given river to be suitable for *D. geminata* presence (Figure 7.3). Including PC1 in the model reduced the deviance indicating an improved model fit and better predicting ability (*P* = 0.993; df = 24). The results show that PC1 can satisfactorily identify sites with maximum likelihood to be with or without *D. geminata*. The three intermediate sites along the PC1 axis are situated on the South shore of the St. Lawrence.

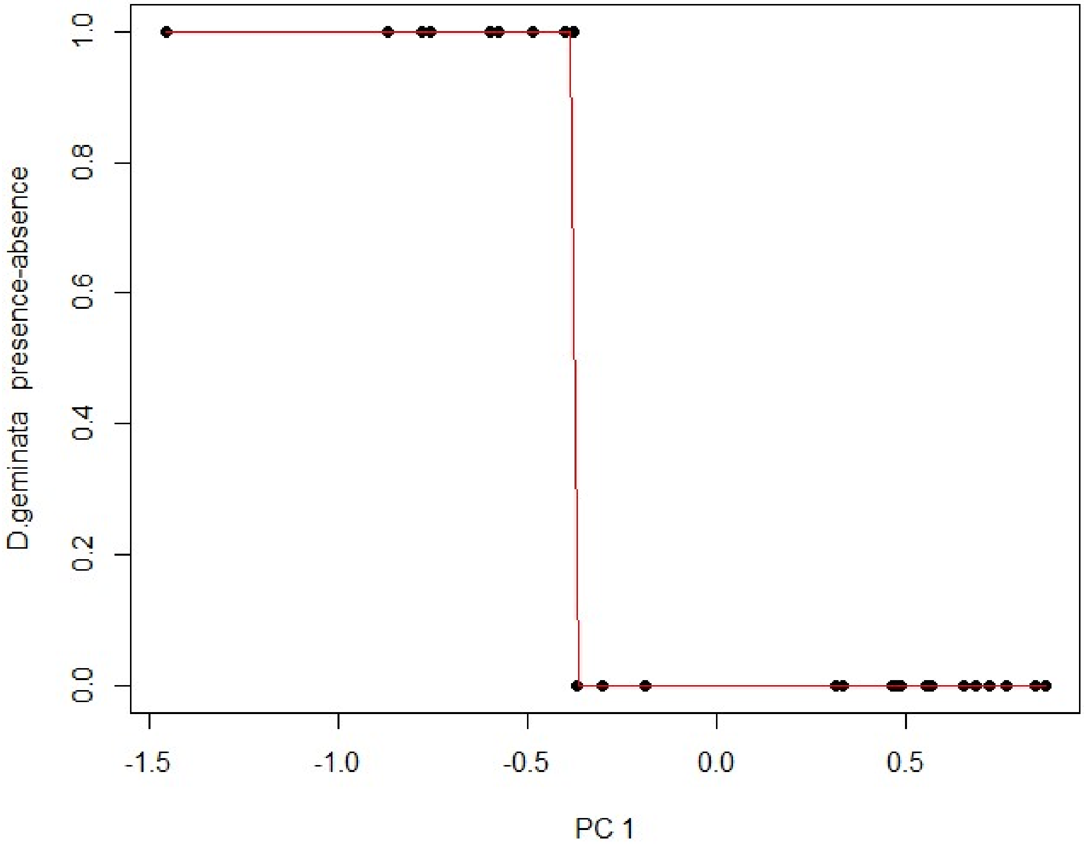

Figure 7.3 **Logistic regression of the PC1 loadings of each river specific to the eight water chemistry parameters (Table 7.3). The model yielded binary probabilities for *D. geminata* presence (1) or absence (0).**

7.4 Discussion

The scope of this case study of Quebec rivers is to build onto the Didymo Conceptual Model elaborated by Cullis *et al.* (2012). Here we established correlations between pH and geology-driven water chemistry parameters and this species spatial distribution in Quebec thus resulting in the identification of key controlling factors for the presence of *D. geminata* cells. In this section, we also present an overview of our results for each water chemistry parameter and provide a review of the existing literature.

7.4.1 pH and geology-driven water chemistry

As proposed by Kumar *et al.* (2009) and tested by Rost *et al.* (2011), water chemistry variables can directly predict *D. geminata* establishment success and distribution in North America. Contrarily to Kuhajek *et al.* (2014) who found that water chemistry of rivers from the North Island and the South Island in New Zealand did not explain *D. geminata* spatial distribution, we found a distinct separation in water chemistry variables between rivers from the North shore and the South shore (Figure 7.2 and Figure 7.3). Rivers from the South shore, where *D. geminata* is present, also displayed higher alkalinity and corresponding higher pH than rivers in regions where *D. geminata* has not been reported. Our results are consistent with Kawecka and Sanecki (2003) as well as with Subakov-Simic and Cvijan (2004) that *D. geminata* presence is associated with higher pH, conductivity, calcium, magnesium, and chlorides. Similarly, in Norway, Lindstrom and Skulberg (2008) found *D. geminata* only in water with sufficiently high calcium and a corresponding pH above neutrality similar to findings from Rost *et al.* (2011) and Richardson *et al.* (2014). pH ranges of South shore rivers are optimal for cell viability and attachment, potentially explaining the current *D. geminata* biogeography in the province of Quebec. In fact, the strongest correlation to predicting *D. geminata* presence in this study is higher pH (~7.9), higher calcium contrations, higher conductivity and clearer water.

Previous studies note that nutrients and, most importantly pH, are controlling factors of diatom distributions due to their sensitivity to specific optimums (Lowe, 1974; Weckstrom *et al.*, 1997; Battarbee et al, 1999; Grenier *et al.*, 2006). Potapova and Charles (2002) stated that in datasets with a wide range of pH values, as in this study, diatoms seem to primarily respond to pH. In fact, in Quebec, Grenier *et al.* (2006) found that pH and conductivity tend to be the main discriminating factors of diatoms communities. The described pH range for *D. geminata,* at the global scale, is slightly below neutral to 9 (Kawecka & Sanecki, 2003; Campbell, 2005; Kilroy *et al.*, 2005; Spaulding & Elwell, 2007; Whitton *et al.*, 2009; Tomàs *et al.*, 2010; Kuhajek & Wood, 2014). Kawecka and Sanecki (2003) found that the most severe nuisance growths were found at pH between 8.1 and 8.3 whereas Lindstrom and Skulberg (2008) found they occurred most frequently in waters with pH above 7.5. In addition, Beeby (2012) tested the viability of multiple water chemistry parameters and found that pH was the only parameter to adversely affect *D. geminata,* although early cell viability studies showed that cells remained intact between 5.9 and 9.9. Kuhajek and Wood (2014), in controlled laboratory settings, found that cell survival was the greatest between pH 7.6 and 8.2 and no attachments or survival was noted below pH 7.4 and above 8.4. Therefore, pH is critical in defining this alga's broad scale distribution and significant in determining establishment success (Kilroy *et al.* 2007).

North shore rivers originate from the Canadian Shield whereas South shore rivers are located in the Appalachians, two contrasting freshwater ecoregions (Berryman, 2006; Abell *et al.*, 2008). The South shore lithology is mainly comprised of calcareous rocks from the Appalachians (Berryman, 2006) thus resulting in higher alkalinity, calcium, conductivity, magnesium, hardness and pH due to chemical reactions between water and bedrock (Corbeil & Néron, 2005). In Quebec, *D. geminata* occurs in catchments with high buffering potential due to sedimentary formation from the Appalachians whereas absence of *D. geminata* was associated with metamorphic and intrusive bedrock geology. Diatom communities in natural environments are primarily influenced by water chemistry (e.g. pH, Conductivity, DOC) reflecting watershed attributes, such as geology, surficial deposits and wetlands (Grenier *et al.*, 2006). These relationships were also observed by Rost *et al.* (2011) in Sierra Nevada, where bedrock geology explained 92% of water chemistry variability and geological calcium was the best predictor for *D. geminata* presence. Elsewhere, Jonsson *et al.* (2008) reported that *D. geminata* was less frequently found in rivers with tertiary basalt bedrock in Iceland. *D. geminata* is known to be prevalent in calcareous rivers in England, Spain (Ellwood & Whitton, 2007; Tomàs *et al.*, 2010) and tends to have a preference for waters with higher geological calcium values. Likewise, in New Zealand, Hammond (2013) found that *D. geminata* was absent in rivers with lower calcium values. Many authors have stated that calcium, and ultimately sulfate and magnesium, are required for stalk adhesion, production and stability (Geesey *et al.*, 2000; Sutherland *et al.*, 2007; Gretz *et al.*, 2008; Lindstrom & Skulberg, 2008; Whitton *et al.*, 2009; Rost *et al.*, 2011; Hammond, 2013; Kuhajek & Wood, 2014; Ehrlich *et al.*, 2016), thus affecting viability of *D. geminata (*Kuhajek *et al.*, 2014).

7.4.2 Sulfates

In Quebec, rivers with *D. geminata* have a higher sulfate concentration (above 4 mg/L) than rivers without. Geology-driven sulfate gradients have also been identified as potential determinants of broad scale *D. geminata* distribution patterns (Lindstrom & Skulberg, 2008; Rost *et al.*, 2011). Further, Lindstrom and Skulberg (2008) found that elevated sulfate (above 2.5 mg/L) seemed to be a prerequisite for *D. geminata.* Richardson *et al.* (2014) also showed that higher sulfate and conductivity could favor *D. geminata* growth.

7.4.3 Conductivity

Conductivity was also a parameter that was higher in *D. geminata*-affected streams. Biggs *et al.* (1990) stated that this metric is positively correlated with siltstone incidence in watersheds and strongly affects periphyton communities. Reports from the western United States indicate that *D. geminata* was found more frequently in environments with lower conductance although the range of this parameter was rather broad (Spaulding & Elwell, 2007). Recent work in the Catskill Mountains of New York state shows that cell density and cover of *D. geminata* was positively correlated with conductivity (Richardson *et al.*, 2014).

7.4.4 Magnesium

Magnesium concentrations were also higher in rivers where *D. geminata* is present. This contradicts observations made by Rost *et al.* (2011) in the Sierra Nevada streams concerning the negative relationship between magnesium and *D. geminata* presence. Higher magnesium concentrations in New Zealand rivers were previously thought to explain the absence of *D. geminata* (Larned *et al.*, 2007) but new results from laboratory analyses corroborate our findings that higher magnesium concentration does not define *D. geminata* absence (Kuhajek *et al.*, 2014).

7.4.5 Color-causing compounds

We found that *D. geminata* presence was inversely associated with dissolved organic carbon (DOC), tannins & lignins, and true color. South of the Saint-Lawrence River, rivers with *D. geminata* show a lower amount of color-causing compounds, such as organic carbon, and clearer water, which supports the theory that high light levels encourage *D. geminata* stalk production (Kilroy *et al.*, 2007; James *et al.*, 2014; Kilroy & Bothwell, 2014; Cullis *et al.*, 2015) since it may be photosynthetically driven under nutrient-limiting conditions (Kilroy & Bothwell, 2012). In New Zealand and Poland, tannin-stained waters with corresponding higher humic acids had unfavorable pH levels and color-causing compounds for *D. geminata* presence (Noga, 2003; Kilroy *et al.*, 2005; Kilroy *et al.*, 2007; Tomàs *et al.*, 2010). DOC was also found to be lower in our studied rivers affected by *D. geminata,* which is in accordance with work conducted by McLaughlin (2009b) in Colorado.

7.4.6 Nitrate and nitrite

Nitrate and nitrite concentrations were found to be higher in the *D. geminata* impacted streams, although remaining relatively low (< 1 mg/L), thereby suggesting that *D. geminata* can prosper in a wide range of nitrogen concentrations (Spaulding & Elwell, 2007; Lindstrom & Skulberg, 2008). Cullis *et al.* (2015) observed a positive correlation between nitrogen concentrations and the presence of *D. geminata* mat in alpine lakes and streams. In phosphorus limited systems, as all the rivers in the present analysis, higher nitrogen concentrations may promote biomass accrual and successful colonization of *D. geminata* (Dodds *et al.*, 2002; Kilroy & Larned, 2016).

7.4.7 Iron

Iron has also been identified as a parameter that would promote *D. geminata* presence and biomass (Sundareshwar *et al.*, 2011). Contradictorily, in Quebec, there is a significant negative trend between iron and *D. geminata* presence (Bothwell *et al.*, 2012). Iron was significantly higher in rivers of the North shore where *D. geminata* has not been reported to produce nuisance level growths indicating that iron is not responsible for this species biogeography in Quebec (Bothwell *et al.*, 2012).

7.4.8 Water chemistry thresholds are scale-dependent

The principal components analysis and associated logistic regression helped define the water chemistry parameters comprising PC1 as the explanatory variables of *D. geminata* presence or absence in Quebec. Our logistic regression approach of *D. geminata* presence or absence in response to water chemistry variables highlights the importance of controls in defining critical thresholds of broad scale biogeography of this diatom. Water chemistry in rivers on the North shore would not be suitable for *D. geminata* establishment because pH is below 7.5 and calcium concentrations are less than 2 mgL^{-1} (MDDEP, 2009). Habitat suitability is key in defining current and potential habitats where *D. geminata* can survive, establish and grow. Rivers located on the south shore without *D. geminata* (3) are all located west of the study area. The Rimouski, Madawaska and Trois-Pistoles rivers, have not been confirmed with *D. geminata* whilst having similar water chemistry to rivers with *D. geminata* presence. However, land use is contrasting and agricultural lands are more abundant in those river catchments. Higher concentrations of phosphorus are suspected to limit *D. geminata* mat presence in these rivers. Therefore, it is likely that these rivers are suitable for *D. geminata* cell viability, but less likely to favor mass production of stalk material due to specific nutrient thresholds.

In this study, some water chemistry parameters had low PCA loadings whereas they had been previously identified as potential driving variables for *D. geminata* distribution, seasonality and persistence in the Didymo Conceptual Model (Cullis *et al.*, 2012). For example, nutrient concentrations are known to affect blooming behavior across various scales (Bothwell & Kilroy, 2011). Many studies do report *D. geminata* growths in low nutrient systems (Spaulding & Elwell, 2007; Lindstrom & Skulberg, 2008; Tomàs *et al.*, 2010; James *et al.*, 2014) while this diatom has been reported in mesotrophic to eutrophic systems with high phosphorus concentration (Kawecka & Sanecki, 2003; Noga, 2003). Nevertheless, within a given ecoregion, the primary causation for stalk production is very low soluble reactive phosphorus (Bothwell *et al.*, 2014). Total Dissolved Phosphorus (TDP) has been found to be inversely related to *D. geminata* percent cover and mat thickness in many regions (Lindstrom & Skulberg, 2008; Miller *et al.*, 2009; Kilroy & Bothwell, 2012; Richardson *et al.*, 2014). All the rivers in our case study have low phosphorus concentrations which are not contrasting between stream sets, thus phosphorus concentrations do not appear to be a determinant driver of *D. geminata* cellular presence-absence across broad geographical scales in Quebec. This is in agreement with Biggs *et al.* (1990) who highlighted that ecoregion-scale determinants of algal communities were climate and geology. Hence, geology-driven water chemistry may define presence-absence of cells across broader ranges than nutrient concentrations which define, at smaller scales, whether stalk production occurs.

Within a given ecoregion, *D. geminata* can display great spatial and inter-annual variability while some rivers have persistent nuisance level mats (Gillis *et al.*, Chapter 6). The importance of threshold dynamics across geographical scales is imperative to consider when defining *D. geminata* biogeography, nuisance levels and habitat window. Thresholds are dynamic and the relative importance of parameters may vary across scales (Potapova & Charles, 2002; Cullis *et al.*, 2012). In support of this statement, a recent study by Falasco and Bona (2013) showed that within each region of Italy, distinct water chemistry parameters were defining the presence-absence of *D. geminata*.

7.5 Conclusion

This study contributes to the progressive increase in knowledge about controlling factors of *D. geminata* growth and shows that contrasting differences in water chemistry can help define biogeography of *D. geminata*. Our results suggest that the distribution of *D. geminata* across landscapes is correlated with water chemistry. Geology-driven water chemistry, notably pH, plays a key role in *D. geminata* occurrence and spatial patterns at the regional scale. Identifying geology based water chemistry as a controlling variable for *D. geminata* reinforces the conceptual model and defines the habitat window for this nuisance diatom. These parameters are assumed to covary at various scales for determining presence-absence but also the extensiveness and seasonality of this mat-forming diatom. Therefore, current distribution of *D. geminata* in North America is more likely defined by critical thresholds that define the habitat window for *D. geminata* rather than recent invasion or spread as suggested by Lavery *et al.* (2014) and Taylor and Bothwell (2014).

Increased knowledge in this species distribution, critical water chemistry thresholds and their drivers are essential for predicting occurrence and severity of nuisance mats towards facilitating management and mitigation measures (Cullis *et al.*, 2012). The investigation of *D. geminata* spatial patterns in Quebec contributes a synthesis of current knowledge on water chemistry thresholds. Nutrient concentrations are an important chemical factor to consider with respect to *D. geminata* cell and stalk production and determining thresholds values will be critical to future management (Tomàs *et al.*, 2010; Cullis *et al.*, 2012; Bothwell *et al.*, 2014).

7.6 Improving the Didymo Conceptual Model: Implications for future research

As defined by other authors and reinforced by this study, water chemistry alone cannot define *D. geminata* biogeography, many controlling variables need to be addressed such as river morphology, flow and substrate stability, light and biological requirements (Kilroy *et al.*, 2008; Whitton *et al.*, 2009; Cullis *et al.*, 2012; Kuhajek *et al.*, 2014).

Precise *D. geminata* distribution maps are needed to elaborate a robust approach to understand how water chemistry and other potential controls vary at local, regional, national and international scales. We acknowledge that a higher resolution map of bedrock and surficial geologies would help identify inter-catchment water chemistry variability. Based on the known current distribution of *D. geminata* in eastern Canada, it is clear that greater efforts are needed towards sampling and detecting. Other regions of Quebec, not investigated here, might be vulnerable to eventual *D. geminata* occurrence. A thorough assessment of presence-absence in Quebec will be needed to clearly determine *D. geminata* cellular presence or absence with molecular-based detection methods such proposed as Cary *et al.* (2014) and Jaramillo *et al.* (2015). Net sampling has also been identified as an accurate method for detecting *D. geminata* cells (Kilroy & Unwin, 2011). By yielding a more precise distribution map and testing correlations with concurrent water chemistry data, it will help refine water chemistry thresholds identified in this study as well as yield better predictive models.

Understanding underlying mechanisms of specific water chemistry variables as controls on the growth and persistence of this mat-forming diatom is necessary. Kuhajek and Wood (2014) have recently tested a large array of water chemistry variables in a controlled laboratory setting. More testing is needed to identify and refine the critical scale-dependent threshold values for *D. geminata*'s habitat window and additional efforts are needed to investigate how ion concentration influences the growth of *D. geminata* and competitive strategy to sustain large amounts of biomass in low-nutrient systems.

Finally, further investigations are also needed to address how thresholds may vary at different spatial and temporal scales. Other specific nutrient thresholds, not presented in this analysis, may also play a role in *D. geminata* colonization success both spatially and temporally. It is important to distinguish cell division and stalk production: specific nutrient thresholds may exist for cells whereas they may be distinctly irrelevant for stalk production (Cullis *et al.*, 2012). In fact, this was recently reiterated by Kilroy (2014) where the relative importance of various chemical and physical thresholds was presented in a hierarchical decision tree for predicting *D. geminata* mat presence and severity in three New Zealand streams. Based on our analysis, we concur that this risk assessment tree for determining habitat suitability for *D. geminata* is applicable to eastern Canadian rivers. We recommend testing the applicability of this prototype in other ecoregions and highlight that this management tool could be used for better predicting *D. geminata* cell presence and nuisance internationally.

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CHAPITRE 8

A PRELIMINARY ASSESSMENT OF THE EFFECTS OF *DIDYMOSPHENIA GEMINATA* NUISANCE GROWTHS ON THE STRUCTURE AND DIVERSITY OF DIATOM ASSEMBLAGES OF THE RESTIGOUCHE RIVER BASIN, QUEBEC, CANADA

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Abstract

In June 2006, blooms of *Didymosphenia geminata* (Lyngbye) M. Schmidt were observed for the first time in the Matapedia River, Quebec. This species can produce nuisance-level epilithic algal mats in oligotrophic rivers with stable flows. The lack of knowledge surrounding the potential impacts of nuisance growths on lotic ecosystems has raised concerns. Periphyton communities were sampled in three rivers of the Restigouche watershed to assess the effects of *D. geminata* nuisance growths on surrounding diatom assemblages. This study provides a preliminary assessment of the effect of *D. geminata* on species composition of diatom assemblages and the influence of increased biofilm complexity on species diversity. Our results show that *D. geminata* mats have an effect on the structure and diversity of diatom assemblages. Conversely, we found no evidence that an increase in Standing Crop Index (SCI) further impacted diatom diversity or structure of these assemblages. This preliminary study contributes to the growing knowledge of the biology of *D. geminata* in lotic environments.

8.1 Introduction

Diatoms often dominate lotic environments and, as primary producers, are essential to the aquatic food web (Patrick, 1977; Round *et al.*, 1990; Burkholder, 2009). Members of a few cymbelloid and gomphonemoid genera produce large amounts of stalk material. To date, *Didymosphenia geminata* (Lyngbye) M. Schmidt is the only freshwater diatom known to produce stalk material that reaches nuisance levels (Blanco & Ector, 2009) in rivers within and outside its native range (Spaulding & Elwell, 2007). *Didymosphenia geminata* was historically considered to be a widespread, but rare species, and was typically found in pristine, oligotrophic streams of North America and Europe (Patrick & Reimer, 1975; Kirkwood *et al.*, 2007; Spaulding & Elwell, 2007). However, reports over the last decade claim that this alga is expanding its ecological range and is an increasing concern (Spaulding & Elwell, 2007; Cullis *et al.*, 2012). *Didymosphenia geminata* is now prevalent in many regions of North America, Europe, and Asia as well as in the southern hemisphere countries of New Zealand, Chile and Argentina (Kawecka & Sanecki, 2003; Kumar *et al.*, 2009; Kilroy & Bothwell, 2011; Sastre *et al.*, 2013). Algal blooms are typically associated with high nutrient levels, but *D. geminata* produces excessive stalk material in low-nutrient waters (Kirkwood *et al.*, 2007; Kilroy & Bothwell, 2012). It also produces more stalk under low phosphorus conditions (Bothwell & Kilroy, 2011), influencing ecosystem function, altering trophic dynamics, biodiversity and water quality (Campbell, 2005; Larned *et al.*, 2007; Spaulding & Elwell, 2007; Blanco & Ector, 2009; James *et al.*, 2010). It has been proposed that *D. geminata* stalks may not be as palatable or nutritious as other algae, and its dominance in lotic systems may reduce food quality and quantity (Larned *et al.*, 2007; Spaulding & Elwell, 2007; Blanco & Ector, 2009).

Early reports of unusual growth of *D. geminata* in Canada were from Vancouver Island (Sherbot & Bothwell, 1993). In eastern Canada, such nuisance growths were first reported in the Matapedia River, in the Gaspésie region of Quebec in 2006 (Gillis & Chalifour, 2010). Since then, there have been reports from all tributaries of the Restigouche River watershed (Figure 8.1). It is estimated that more than 75% of the rivers in the Gaspésie region now present occasional to persistent *D. geminata* macroscopic growths (MDDEP 2010; Gillis, unpublished data). In the Matapedia River, the stalk material and associated microbial matrix may become several centimeters thick, cover 100% of the riverbed and extend up to 35 km along the river (Gillis & Chalifour, 2010).

In response to public concern about additional stress on Atlantic salmon (*Salmo salar*) populations, efforts to assess *D. geminata* impacts on the trophic dynamics of eastern Canadian rivers were initiated. Concern is largely the result of a lack of knowledge of the impact of *D. geminata* on other aquatic organisms. Initial research in eastern Canada focused on the macrobenthic community structure (Gillis & Chalifour, 2010). Results showed that the presence of *D. geminata* increased invertebrate densities, but significantly shifted proportions of large taxa (e.g. mayflies, stoneflies and caddiesflies) toward smaller taxa (e.g. chironomids). In Sierra Nevada streams of California such growths of *D. geminata* have been characterized by Rost (2010) as an "ecologically disruptive algal bloom" (EDAB). Large amounts of stalk material are thought to compromise the sustainability of stream ecosystems (Cullis *et al.*, 2012). Gretz (2008) mentioned that stalks of *D. geminata* formed a "woven fabric" mat entrapping algae, macroinvertebrates and detritus. Roemer *et al.* (1984) had previously discussed that diatom mucilage increased the surface area for attachment in periphyton communities, harbouring small diatoms. Electron micrographs of *D. geminata* stalk material confirm that the stalk matrix creates a microenvironment where numerous small diatoms are attached (Kilroy *et al.*, 2006; Spaulding & Elwell, 2007). *Didymosphenia geminata* and its stalks have been reported to skew algal community structure and form more homogenous assemblages (Spaulding *et al.*, 2010), leading to lower diversity and evenness (Larson & Carreiro, 2008).

In order to investigate the influence of *D. geminata* and its stalks on surrounding diatom assemblages, this study aims to address the questions, 1) Do diatom assemblages differ between areas with and without *D. geminata*? 2) Are diatom assemblages modified over a *D. geminata* extracellular stalk material gradient due to increased biofilm complexity?

8.2 Materials and methods

8.2.1 Study Area

The Restigouche River watershed, with a drainage area of more than 10,000 km^2, is an interprovincial catchment of eastern Quebec and northern New Brunswick. This catchment is comprised of large tributaries as well as numerous small cold-water streams with neutral to slightly alkaline pH values. Nuisance levels of stalk material produced by *D. geminata* have been reported since 2008 in all tributaries of the main Restigouche River (Gillis, unpublished data). In this study, the Restigouche River and two of its tributaries, the Patapedia River and Gagnon Brook, were sampled in 2010 and 2013 (Figure 8.1). Selected sites of the Patapedia and Restigouche rivers had similar water depths, substratum size and stability, while Gagnon Brook, a third order tributary, had a smaller wetted width and greater canopy cover. All samples were collected from riffles and no high flow events had occurred in the month prior to sampling.

8.2.2 Periphyton Sampling

Rock scrapings were initially collected as part of a preliminary assessment of the effects of *D. geminata* on diatom assemblages. On 21 July 2010, four rocks were selected for collection and combined into one composite sample for each sampling site. At site PAT2M (Figure 8.1), a composite sample was collected from rocks showing notable colonization by *D. geminata* (i.e. 50-80% cover of the rock with a mat thickness of 10 mm). Within four meters of the first sample, a second composite sample was collected from rocks showing no visible colonization by *D. geminata*. On the same sampling day, at site RGBW, four samples were collected from rocks showing contrasting degrees of *D. geminata* accrual; thin mats (two rocks with an average mat thickness of 6 mm) versus thick mats (two rocks with an average mat thickness of 13 mm).

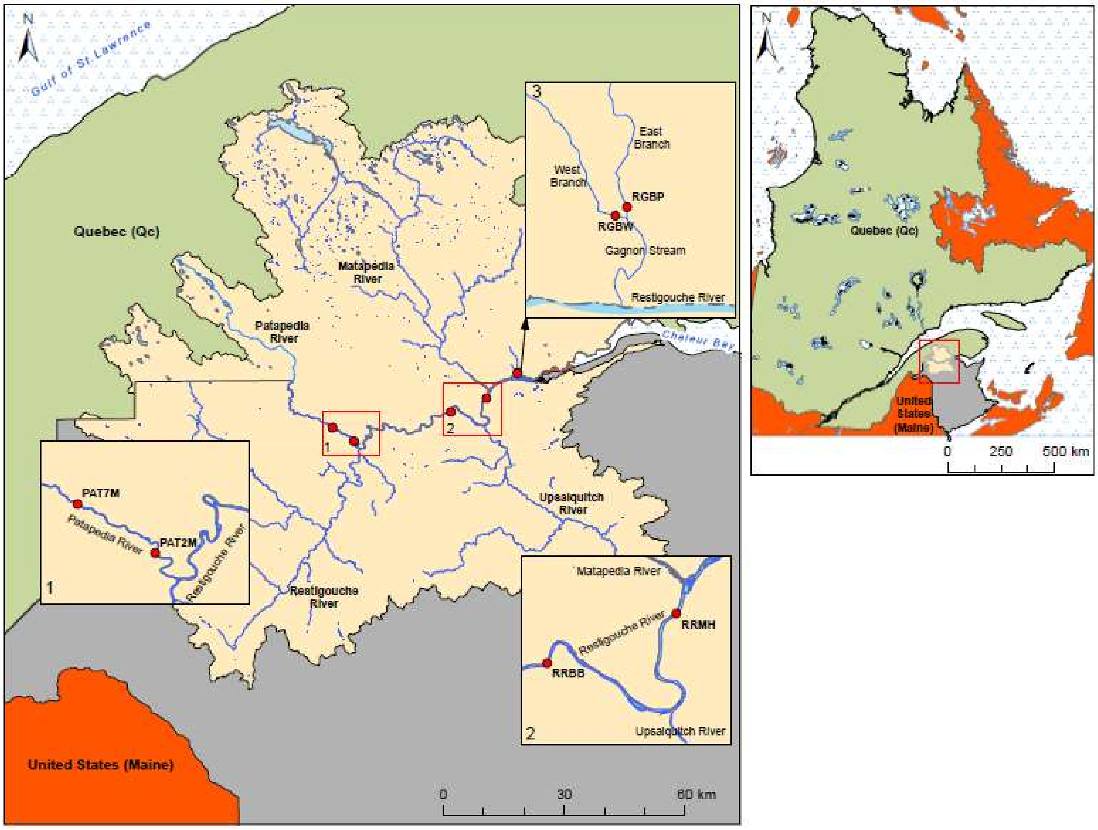


Figure 8.1 **Study area and sampling site location distribution throughout the Restigouche River watershed, eastern Quebec, Canada**

Following preliminary analyses of the 2010 samples, the need for further investigation was evident. Therefore, in 2013, a total of six sites were selected throughout the Restigouche watershed (Figure 8.1). Between 18-21 June six rocks of similar size and surface texture presenting a gradient of *D. geminata* accrual were removed from the streambed at each sampling site. Rock scrapings of the periphyton, circumscribed by a 62-mm delimiting circle placed over the surface of each stone (Kilroy *et al.*, 2006), were sampled (n = 36). The Standing Crop Index (SCI) was determined for each rock by measuring mat thickness and estimating percent cover of the sampled area. The SCI is a standardized method for quantification of *D. geminata* mat development (Kilroy & Bothwell, 2011). Samples were preserved with Lugol's solution and transported to the lab for later processing.

8.2.3 Sample preparation, microscopical observation and statistical analyses

All samples were homogenized before sub-sampling for organic matter digestion, using nitric and sulfuric acids (1:1) heated to boiling for one hour. The acids were removed through centrifugation and dilution to neutral pH. The cleaned samples containing the diatom frustules were then mounted onto coverslips and attached to microscope slides using Naphrax mounting medium. A minimum of 400 diatom valves were counted at a magnification of 1250x and identified at the lowest possible taxonomic level (Lavoie *et al.*, 2008). Diatom data are expressed as relative abundances for subsequent statistical analyses. The Shannon diversity index was calculated and non-metric multidimensional scaling (on square root transformed data) were conducted using PRIMER v. 6 (Clarke & Gorley, 2006). ANOVA and t-test were conducted in Systat v. 12 (San Jose, CA, USA).

8.3 Results

8.3.1 Diatom assemblages from samples with and without *D. geminata* colonization

Comparison of assemblages collected at site PAT2M in 2010 showed that the most common diatom taxa (defined as all species occurring at > 2%) were present in both composite samples (Figure 8.2). Regardless of *D. geminata* presence, *Achnanthidium minutissimum* (Kützing) Czarnecki was the most abundant taxon. The relative abundances of taxa in the two samples differed slightly. For example, *Fragilaria capucina* Desmazieres and *Diatoma ehrenbergii* Kützing were more abundant in the *D. geminata* sample (10% and 6%, respectively) than in the sample collected from rocks with no visual accrual of *D. geminata* (5% and 3%, respectively). Diatom richness and diversity were slightly higher in the presence of *D. geminata* biomass (21 taxa and Shannon's diversity index of 1.46 with *D. geminata* compared to 19 taxa and Shannon's diversity index of 1.38 without).

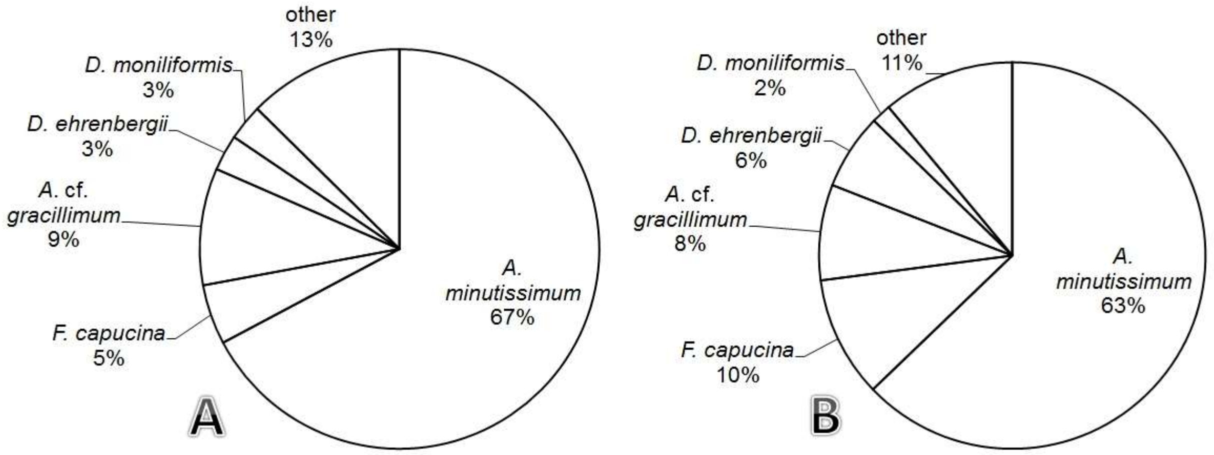


Figure 8.2 **Relative abundance of the most common taxa observed in the samples collected on the rocks showing *D. geminata* biomass (A) and on the rocks showing no visual accumulation of *D. geminata* (B)**

8.3.2 Diatom assemblages from samples with thin versus thick *D. geminata* mats

Analyses on the samples collected at RGBW in 2010 (rocks with contrasting *D. geminata* mat thicknesses) showed different assemblages between 6 mm and 13 mm mats. For example, both samples collected from 6 mm mats comprised predominantly species of the *A. minutissimum*-complex (75% and 70%), and small specimens belonging to the *F. capucina* var. *vaucheriae*-complex (19% and 20%). Contrastingly, the samples collected from the 13 mm mats had lower abundances of the *A. minutissimum*-complex (36% and 41%) and higher abundance of the small *F, capucina* var. *vaucheriae*-complex (36% and 42%). There was less than 1% *Diatoma moniliformis* Kützing on the 6 mm mats, but 8% and 5% on the thicker mats. The diatom assemblage data are presented in Appendix 1 for taxa representing more than 1% in at least one sample. Species richness and Shannon's diversity index were lower on rocks with thinner *D. geminata* mats (richness: 13 and 13; Shannon's diversity index: 0.79 and 1.02) compared with thicker mats (richness: 21 and 16; Shannon's diversity index: 1.75 and 1.47).

These preliminary comparisons of diatom assemblages from the Patapedia River (presence versus absence of *D. geminata*) and Gagnon Brook (thin versus thick *D. geminata* mats) also revealed low relative abundances of *D. geminata* (0% to 2%). Despite the fact that it was sometimes not recorded in a 400 valve count, cells of *D. geminata* were observed on all slides.

8.3.3 Diatom assemblages from contrasting *D. geminata* SCI levels

Table 8.1 presents the range of SCI values measured at each sampling site in 2013. The gradient of *D. geminata* extensiveness was scored 1-6, where 1 corresponds to the highest SCI value and 6 corresponds to the lowest *D. geminata* accrual at each sampling site. *Didymosphenia geminata* cells were not recorded (400 valve counts) in all the samples (n = 36) despite the substantial biomass accrual. The highest relative abundance of *D. geminata* was observed at PAT7M for SCI levels 4 and 5, with values of nearly 4%.

Table 8.1 Range and SCI values for each of the six *D. geminata* accrual levels of the 2013 sampling effort

Site	SCI range	1	2	3	4	5	6
PAT2M	0.5–285	285	260	105	50	20	0.5
PAT7M	1–500	500	225	150	62,5	30	1
RGBP	15–1300	1300	800	450	250	60	15
RGBW	7.5–700	900	525	400	180	150	7.5
RRBB	4–180	180	150	100	50	40	4
RRMH	21–1000	1000	525	480	160	100	21

Several diatom taxa (94 species and complexes) were observed in the samples from the six sites. The assemblage data are presented in Appendix 2 for the taxa representing more than 1% in at least one sample. The most common diatoms belonged to the *A. minutissimum*-complex, relative abundance > 80% at RGBW on rock with SCI level 6 biofilm. *Achnanthidium* cf. *gracillimum* (Meister) Lange-Bertalot and *Achnanthidium* cf. *deflexum* (Reimer) Kingston were also common, more than 40% in certain samples. *Diatoma moniliformis*, *Diatoma ehrenbergii*, *Hannaea arcus* (Ehrenberg) Patrick, and *F. capucina* var. *vaucheriae*-complex were also common, as well as the Cymbellaceae represented by *Encyonema silesiacum* (Bleisch) Mann, *Encyonema minutum* (Hilse) Mann, and *Delicat*a cf. *delicatula* (Kützing) Krammer. Species belonging to *Gomphonema* were very rare in our study, and all the cymbelloids were small, non-stalk-producing species.

Shannon's diversity index was calculated for each sample and values are presented as box-plots for each SCI level (Figure 8.3). A one-way ANOVA showed no significant difference in diversity between the six levels of *D. geminata* SCI ($F_{(5, 30)} = 1.45$, *p-value* = 0.24, n = 36). Although not significantly different, the graph suggests a lower diversity for SCI level 6 (Figure 8.3).

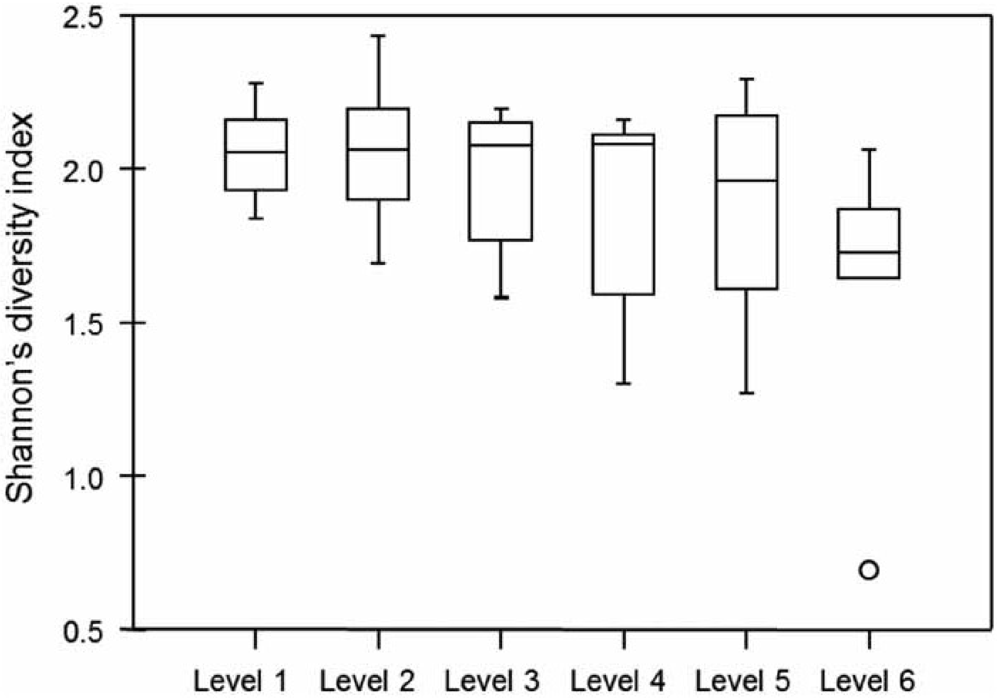


Figure 8.3 **Box-plot of the Shannon's diversity values for each SCI level. The empty circle represents a far outside value.**

Despite the fact that most of the common taxa were observed across all levels of *D. geminata* accrual and that no significant difference was observed in diversity, the assemblage structure seems to show some variability between the different SCI levels. For example, with low visual accrual of *D. geminata* (SCI level 6) RGBW had 83% *A. minutissimum*-complex and 9% *D. moniliformis*, while the greatest accrual (SCI level 1) had 34% and 33% of these taxa respectively. At all sites, the relative abundance of fragilarioid taxa increased with increasing *D. geminata* mat biomass. Apart from this there were no marked differences and consistent patterns in diatom assemblages across the gradient of mat extensiveness. This can be seen from Figure 8.4 showing the distribution of samples based on a non-metric multidimensional scaling plot of Bray-Curtis similarities (2D stress = 0.14).

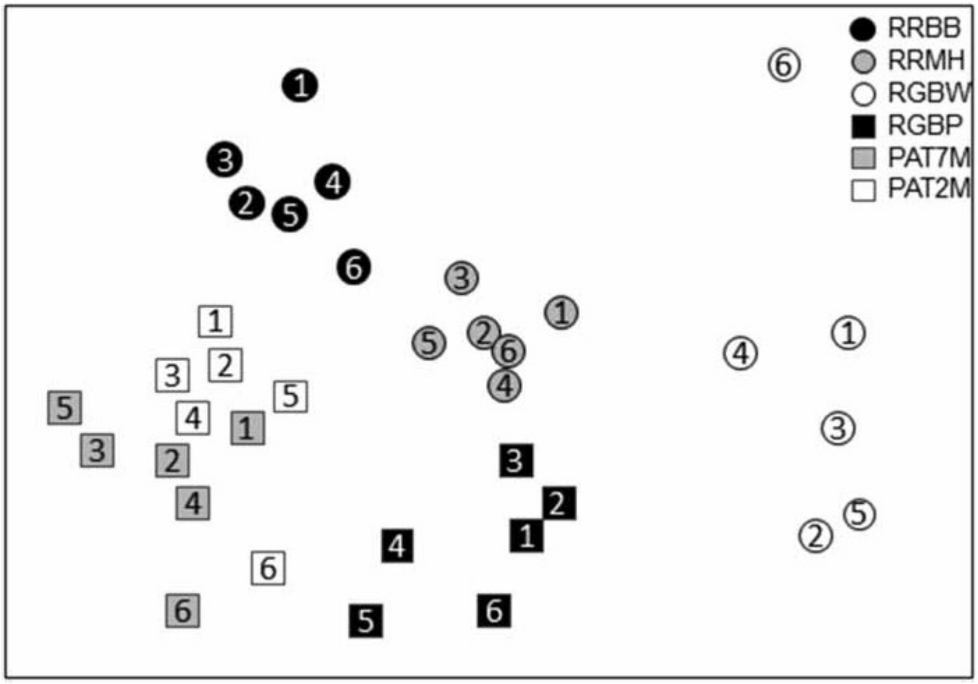


Figure 8.4 **Non-metric multidimensional scaling plot representation of Bray–Curtis similarities among each SCI level and across all sites. The number in the symbol represents the accrual of *D. geminata*, whereas SCI level 6 corresponds to the lowest SCI value and level 1 corresponds to the highest (refer to Table 8.1).**

This sample distribution does not reveal any strong pattern that could suggest that the assemblages are markedly different for specific SCI levels. However, we noticed a weak trend for three sites (RGBW, PAT2M and PAT7M) where the similarity among SCI levels 1 to 5 seemed stronger compared to level 6. SCI level 6 at RGBW had a much lower relative abundance of *D. moniliformis* and a higher relative abundance of *A. minutissimum* compared to the other SCI levels. At PAT2M, SCI level 6 seemed less similar than the other SCI levels due to higher relative abundances of *A. minutissimum* and *A*. cf. *deflexum* and lower relative abundance of *E. silesiacum*. SCI level 6 at site PAT7M showed a higher relative abundance of *A*. cf. *deflexum* and a lower relative abundance of *E. silesiacum* than for the other levels of *D. geminata* biomass. This suggests that, for half of our sites, assemblages found on rocks with very low *D. geminata* SCI values were less similar than the assemblages found on rocks presenting higher *D. geminata* growth. The results also showed that the variability in the diatom assemblages seem to be mainly attributed to the different sites than to the different SCI levels. This trend was further explored by running a t-test (for two groups of unequal sizes and unequal variances) on Bray-Curtis similarities where the values for SCI levels 1 to 5 (n = 60; mean Bray-Curtis similarity = 72.3) were compared with those for SCI level 6 (n = 30; mean = Bray-Curtis similarity = 66.4). The results showed a significant difference between the two groups (t = 3.25;

$p < 0.01$) indicating that the Bray-Curtis similarity values were indeed significantly higher when comparing diatom assemblages collected on rocks presenting pooled SCI levels 1 to 5 with SCI level 6, than when comparing the assemblages from all SCI levels individually.

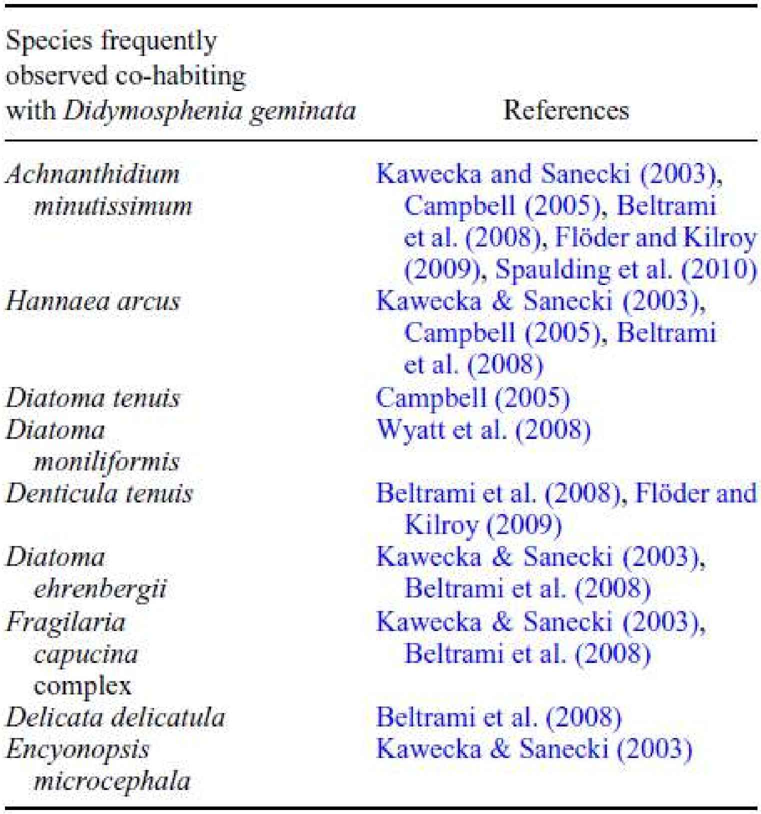
8.4 Discussion

8.4.1 Presence of *D. geminata* mats and its effect on species composition and diversity

The low relative abundance of *D. geminata* cells observed in the present study is in agreement with several studies, where *D. geminata* relative abundance was less than 3% (Spaulding & Elwell, 2007; Beltrami *et al.*, 2008), even within sites with extensive *D. geminata* stalk material. Although numbers of *D. geminata* cells are low, this could still represent up to 85% of the total diatom cell biovolume (Jonsson *et al.*, 2000). However, this is only a rough estimate because it depends heavily on the biovolume of the other diatom species in the assemblage observed by Jonsson *et al.* (2000) compared to the present study. The reason for this apparent discrepancy between abundance and biovolume is that *D. geminata* has much larger cells (80-150 µm in length) but smaller species dominate the diatom assemblage numerically. Despite thick biofilm accrual, the very low relative abundance of *D. geminata* is the result of extensive stalk biomass rather than cell numbers. This mucilaginous material creates a habitat for many other smaller diatom species and other microorganisms (Domozych *et al.*, 2010), which far exceed *D. geminata* cells in numbers. An interesting observation is that the relative abundance of *D. geminata* cells was not maximum where mats were thickest. This suggests that the high stalk biomass produced by *D. geminata* offers an ideal environment for colonisation by other small diatom species that become more abundant so that the relative abundance of *D. geminata* declines. A similar result was obtained by Flöder and Kilroy (2009) in New Zealand where the *D. geminata* colonies were completely overgrown by native species.

Most of the common taxa (and some less common ones) observed in our study have also been found co-habiting with *D. geminata* in other studies (Table 8.2). In agreement with our results, Rost (2010) and Spaulding *et al.* (2010) also found *D. geminata* to typically co-occur with achnanthoid and fragilaroid species, while rarely co-occurring with gomphonemoid and larger cymbelloid taxa.

Table 8.2 **List of common diatom taxa observed in the present study that are frequently found co-habiting with *D. geminata* in other countries**



Species frequently observed co-habiting with *Didymosphenia geminata*	References
Achnanthidium minutissimum	Kawecka and Sanecki (2003), Campbell (2005), Beltrami et al. (2008), Flöder and Kilroy (2009), Spaulding et al. (2010)
Hannaea arcus	Kawecka & Sanecki (2003), Campbell (2005), Beltrami et al. (2008)
Diatoma tenuis	Campbell (2005)
Diatoma moniliformis	Wyatt et al. (2008)
Denticula tenuis	Beltrami et al. (2008), Flöder and Kilroy (2009)
Diatoma ehrenbergii	Kawecka & Sanecki (2003), Beltrami et al. (2008)
Fragilaria capucina complex	Kawecka & Sanecki (2003), Beltrami et al. (2008)
Delicata delicatula	Beltrami et al. (2008)
Encyonopsis microcephala	Kawecka & Sanecki (2003)

Higher diversity values with higher *D. geminata* accrual were observed in our preliminary study in 2010 and also from the 2013 samples (although the trend was not significant), which suggests that the polysaccharide matrix produced by *D. geminata* may favour the colonisation by a larger number of species. This result contradicts that from Larson and Carreiro (2008) who reported diversity and evenness to be lower at sites impacted by *D. geminata* blooms. Overall, most studies (e.g. Larson, 2007; Wyatt *et al.*, 2008; Spaulding *et al.*, 2010; Falasco & Bona, 2013) show a strong effect of *D. geminata* colonisation. On the other hand, preliminary observations by Beltrami *et al.* (2008) found that *D. geminata* did not significantly impact composition or diversity of the diatom assemblage. Our study suggests changes in assemblage structure in the presence of *D. geminata*; shown by both the presence-absence and the thin versus thick mat comparisons. There was also a weak trend with SCI level, where the results suggested that the assemblages were more similar among samples collected on rocks with substantial *D. geminata* accrual compared with the samples collected where *D. geminata* was minimal (SCI levels 1-5 compared with SCI level 6). These results suggest that, past a certain *D. geminata* accrual, increase in biofilm SCI does not have a greater impact on the structure of the assemblage. Thus, there seems to be a greater effect of *D.*

geminata nuisance growths on diatom assemblage composition when comparing presence-absence and very low visual accrual versus any other SCI level.

The lack of strong and clear effects of *D. geminata* on diatom composition suggests that there was no shift towards more cosmopolitan and more tolerant diatoms as suggested by Larson (2007). Rahel (2002) observed a reduction in overall aquatic biodiversity and the replacement of native by non-native species, while Burkholder (2009) suggested that *D. geminata* growth could exclude species that formerly occupied the habitat. Such assemblage homogenization was not observed in our study where common species observed remained the same amongst all SCI levels.

8.5 Conclusion

This preliminary descriptive study revealed small scale effects of *D. geminata* mat presence on diatom assemblages throughout the Restigouche River watershed. This work contributes to the growing knowledge of *D. geminata* ecology and of impacts that nuisance growths may have on lotic environments. In addition, this is the first study to describe *D. geminata* effects on diatom diversity and abundance, as well as assessing how increasing SCI values may influence diatom assemblages in eastern Canada.

Our preliminary tests (2010) suggested slight modification of assemblage structure and higher diversity in the presence of *D. geminata* mats, while the samples collected in 2013 using a more elaborate sampling design did not yield such clear evidence. This may be due to the lack of replicate samples (only one sample per SCI level was collected at each of the six sites), which may have increased variability and masked particular trends. We acknowledge that further data are needed for a more robust analysis. Increasing n values and replication would improve statistical power and, therefore, further support our findings. For example, Hollingsworth and Vis (2010) recommend sampling at least two riffles per watercourse in order to attain representative samples for periphyton assemblages.

Further research is necessary to evaluate how percent cover, thickness and mat persistence affect the magnitude of changes in diatom assemblages as well as on higher trophic levels (Bothwell & Spaulding, 2008; Gillis & Chalifour, 2010). Abiotic factors may influence dynamic states of *D. geminata* (Cullis *et al.*, 2012). Seasonality and successional stage of the periphyton community is most likely to define the diatom diversity and relative abundance in a given reach. The impact of *D. geminata* nuisance growths may therefore be variable across landscapes and seasons. Our preliminary study does not take seasonal changes of algal assemblages into account and it would be interesting to look at change over time and assess how assemblages change with decreasing mat conditions. Given the increasing concern and occurrence of algal blooms related to global change, (Power *et al.*, 2009) research efforts are necessary to understand *D. geminata* ecology and impacts to improve management of inland waters internationally.

Acknowledgements

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CHAPITRE 9

SHIFTS IN JUVENILE ATLANTIC SALMON (*SALMO SALAR)* FORAGING BEHAVIOUR DRIVEN BY THE PRESENCE OF *DIDYMOSPHENIA GEMINATA* MATS

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Version à être soumise pour publication

Abstract

Didymosphenia geminata (didymo) produces thick benthic mats in oligotrophic rivers worldwide. In the last decade, these proliferations have occurred in eastern North America most notably in the Restigouche River watershed. Recent research showed that *D. geminata* mats can cause significant shifts to macroinvertebrate community structure and prey abundance. Despite an increase in overall prey densities, prey location and availability to juvenile Atlantic salmon (JAS) may be altered. The research objectives aimed at assessing JAS foraging behaviour as well as prey availability in sites with contrasting mat accruals. Results show that JAS make a higher proportion of benthic forays than drift forays with increasing *D. geminata* percent cover ($p < 0.001$) and the resulting multiple regression model indicates that benthic foraging is driven by *D. geminata* mat severity, invertebrate drift density and flow (adjusted $R^2 = 0.60$). JAS showcased behavioural plasticity and opportunistically modified their foraging behaviour in response to changing habitat and food supply conditions driven by *D. geminata* mats.

Keywords: foraging behavior, *Didymosphenia geminata*, *Salmo salar*, benthic foray, drift-feeding salmonid, macroinvertebrate, prey

Foreword:

This chapter presents foraging behaviour and drifting prey data exclusively. Benthic prey data exist although it is not included in the current chapter due to time constraints.

9.1 Introduction

Since 2006, nuisance growths of *Didymosphenia geminata* (Lyngbye) M. Schmidt have been recurrently occurring in eastern North America, most notably in several of the Atlantic salmon (*Salmo salar*) rivers of the Gaspe Peninsula. Because this diatom often forms thick and extensive benthic mats, there are concerns that it may act as an additional stressor on Atlantic salmon *(Salmo salar)* populations on which most of the regional economy relies through its sport fishing industry (Whoriskey, 2008).

D. geminata has been shown to alter the structure of macroinvertebrate communities through a reduction of EPT taxa (Ephemeroptera, Plecoptera, Trichoptera) proportions relative to chironomids (Gillis & Chalifour, 2010; Kilroy *et al.*, 2010). Although benthic macroinvertebrate densities are increased in presence of *D. Geminata,* it has been suggested that it could limit the entrainment and drift of preys available for drift-feeding salmonids (Shearer *et al.*, 2007). Such shifts in the structure and availability of preys could in turn affect the diet (Shearer *et al.*, 2007; Gillis & Chalifour, 2010; James *et al.*, 2011) and feeding behaviour of salmonids.

Although juvenile Atlantic salmon (JAS) predominantly feed from drifting invertebrates (Elliot, 1973; Rader, 1997; Nislow *et al.*, 1998), they are opportunistic foragers that have been shown to modify their feeding behaviour in response to changing habitat conditions and food supply (Wankowski & Thorpe, 1979; Gibson, 1993; Nislow *et al.*, 1998; Amundsen *et al.*, 1999). Considering *D. geminata*'s potential impact on resource availability, we hypothesized that JAS would alter their foraging behaviour in presence of this alga. This study therefore aimed at assessing JAS feeding behaviour as well as evaluating drifting and benthic prey availability in contrasting levels of *D. geminata* accrual and extent.

9.2 Methodology

9.2.1 Study area

The study was conducted on the Patapedia River, a gravel-bed tributary of the Restigouche River (Quebec and New Brunswick, Canada) (Figure 9.1). The area of this forested catchment is 782 km^2. *D. geminata* was first reported in 2007 and has since been occurring on a regular annual basis.

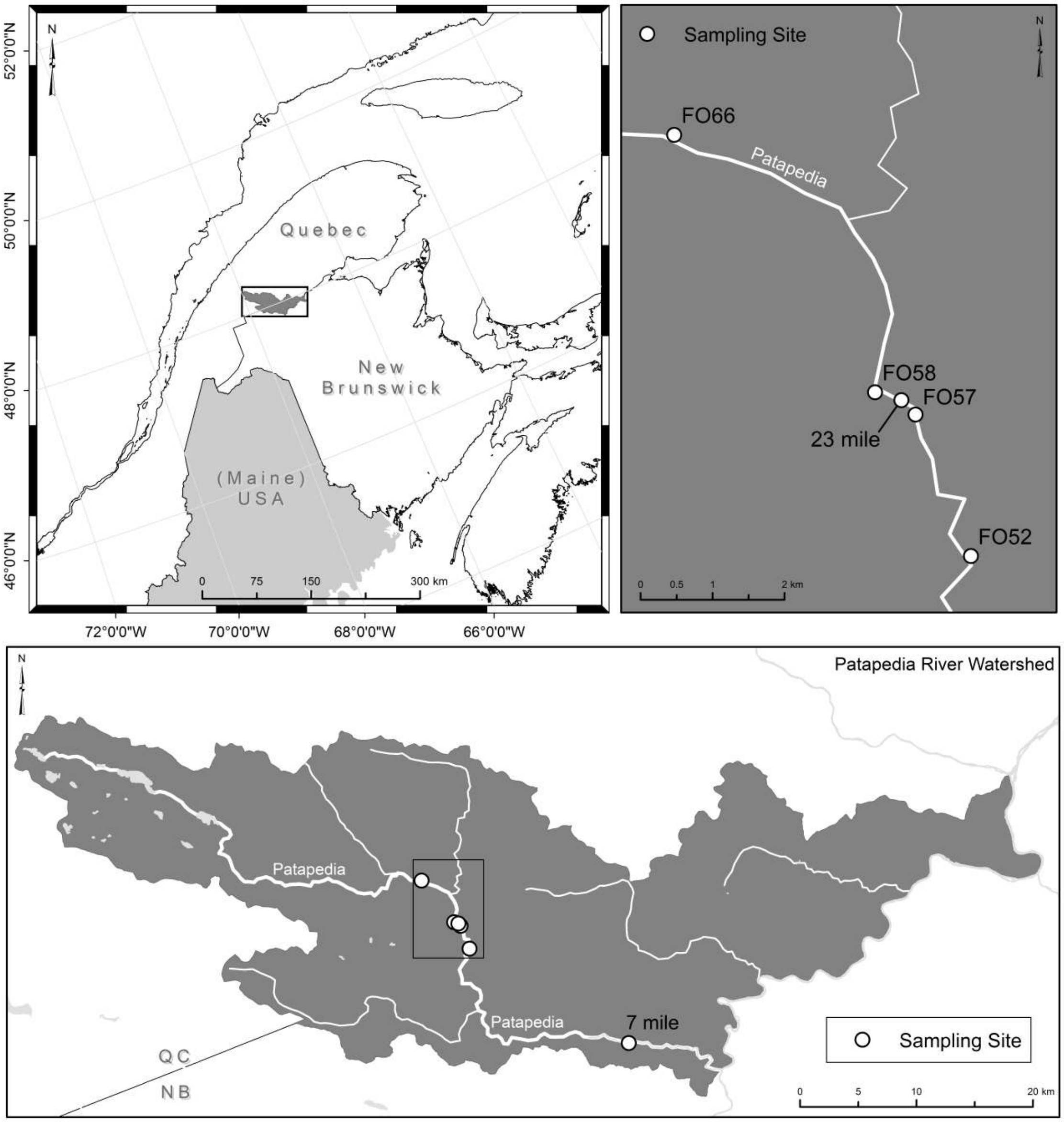

Figure 9.1 Location of the Patapedia River (Quebec, Canada) and of the six sampling sites retained for foraging behavior assessment

9.2.2 Sampling sites and events

Juvenile salmon foraging behaviour data was collected at the beginning and end of summer 2010. Between June 23 and July 8, a total of 49 fish observations were obtained from six different sites (Figure 9.1) selected for their similar physical habitat conditions in terms of flow velocity, water depth, substrate size, and water temperature, but highly contrasting percentages of *D. geminata* cover (Table 9.1). At the end of summer, between August 17 and September 1, 28 additional observations were obtained from three of the six early summer monitoring sites (Table 9.2). The decision to sample a reduced number of sites was taken in view of the absence of *D. geminata* from all original six sites, and because the three selected sites adequately represented the range of habitat conditions in the absence of *D. geminata* covers.

Table 9.1 **Range of habitat characteristics during the early summer sampling event for each site on the Patapedia River**

Site	Mean flow (cm/s)	Mean depth (cm)	Mean substrate size (B axis) (cm)	Mean temperature (°C)	*Dg* range (%)
FO66	30.1	34.9	7.0	15.5	0
FO58	40.9	37.8	8.9	15.0	5-85
23 mile	58.6	49.1	7.2	19.2	12.5-30
FO57	39.2	44.4	7.9	16.3	5-30
FO52	47.2	57.6	9.6	16.2	12.5-75
7 mile	52.2	44.0	10.7	16.4	20-60

Table 9.2 **Range of habitat characteristics during the late summer sampling event for each site on the Patapedia River**

Site	Mean flow (cm/s)	Mean depth (cm)	Mean substrate size (B axis) (cm)	Mean temperature (°C)	*Dg* range (%)
FO66	18.0	43.8	6.9	16.75	0
FO57	25.6	41.4	8.0	17.4	0
7 mile	40.5	30.0	9.1	22.7	0

9.2.3 Foraging Behaviour data collection

The foraging behaviour of young-of-the-year salmon was obtained by focal-fish observations conducted by a single snorkeler using a protocol adapted from Dionne and Dodson (2002) and Cunjak and Power (1986). All observations were carried out between 0800 and 1700 h, when JAS are known to be most active (Wankowski, 1979; Stradmeyer & Thorpe, 1987; Nislow *et al.*, 1998; Breau, 2003). Precautions were taken to ensure that fish were not disturbed before the beginning of the sampling session. For each session, the snorkeler entered the downstream end of the reach and proceeded upstream while making transects perpendicular to the river bank. When a fish was located, it was observed for 1 minute to ensure that its behavior was not influenced by the presence of the observer. A minimum distance of 1.5 m was maintained at all time between the observer and the fish, and if this distance was accidently not respected, the observation was not included in the analyses. The behaviour of the fish was then observed for a period of 15 minutes while the diver remained motionless. During this period, a continuous record of fish behavior was obtained by classifying it according to one of the following category: moving, stationary, feeding, hiding, territoriality. The feeding behaviour was classified as either drift or benthic foray (Table 9.3). Each behavior type corresponded to an audio code communicated by the observer through the snorkel and recorded with a hand-held recorder by an assistant. After the observation session was complete, the fish was gently directed in the downstream direction to ensure it would not be observed more than once.

A colour-painted rock was placed at each location where a fish was observed for subsequent habitat measurements. Water depth was determined with a meter stick. Flow velocity was measured for 60 sec with an ADV-Flowtracker positioned at a distance above the bed corresponding to 40% of the water depth. Mean substrate size was obtained by measuring and averaging the b-axis of 9 randomly sampled bed particles over the observation area (Figure 9.2).

Table 9.3 **Definitions of recorded behaviour categories of juvenile Atlantic salmon (*Salmo salar*) during observation periods**

Behaviour	Description
Moving	A swimming motion longer than half the body length, which results in displacement from a position
Stationary	Holding position near the substrate; it includes movements shorter than half of the body length of the fish
Drift foray	Direct movement upward to intercept a drifting particle in the water column, followed by a return to the original position. The fish's mouth does not make contact with the substrate.
Benthic foray	Direct movement downward towards the substrate followed by a return to the original position. The fish's mouth does contact the substrate to grasp a benthic dwelling prey item.
Refuge	Fish moving to seek cover to hide under a substrate particle
Territoriality	An aggressive movement directed towards another fish in order to defend its territory

Modified from Dionne and Dodson (2002) and Nislow *et al.* (1998).

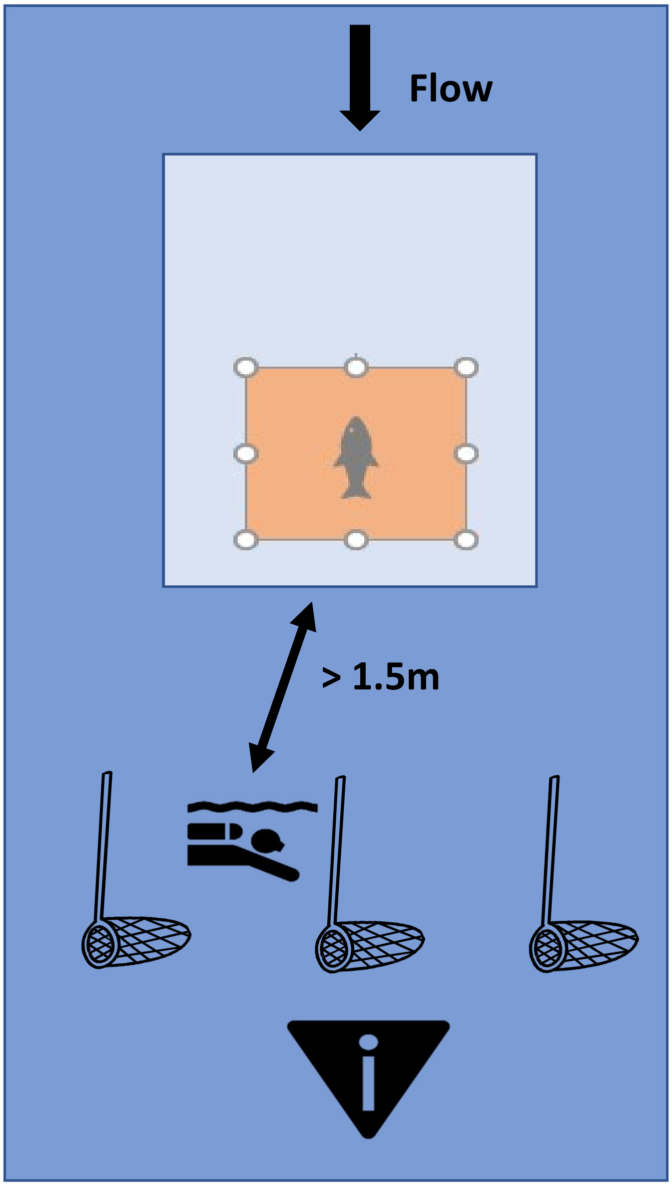

Figure 9.2 An invertebrate drift-net was positioned at the downstream end of the reach 24 h prior to observations. After drift-net retrieval, a composite sample included 3 D-nets samples of benthic invertebrates. Foraging behaviour observation diagram showcasing the downstream position of the observer maintaining a minimal distance of 1.5 m with the JAS. The dark blue rectangle represents the river reach with direction of flow. The light blue rectangle presents the area surveyed for *D. geminata* percent cover (1 m from either side of the fish, 0.5 m downstream and 1.5 m upstream from the fish). The orange square (1 m^2) represents the surveyed habitat for substrate size, where each white circle corresponds to a measurement (n = 9). Flow and depth was measured at the center corresponding to the JAS location.

9.2.4 Prey availability in drift and benthos

Prior to conducting snorkelling observations, a 30 cm X 30 cm drift net (600-µm mesh size) was installed at the downstream end of each sampling site and allowed to sample drifting invertebrates for a period of 24 hours before the beginning of fish behaviour observations. Water velocity at the entrance of the drift net was measured at installation and retrieval of the net with a Handheld ADV-Flowtracker. The two velocities were then averaged and used to estimate the volume of water filtered by each drift net during the 24 h sampling period. Following drift-net retrieval, three benthos samples were collected with a 42-cm wide D-net (600-µm mesh size) directly upstream from the drift net location and pooled into a composite sample for the site. A total of 12 drift net samples and 12 benthos samples were collected, corresponding to 12 behavioural observation days. All samples were preserved with 90% ethanol and, upon return to the laboratory, invertebrates were sorted, enumerated and identified at family level (Merritt & Cummins, 2008).

9.2.5 Metrics calculation

Drift density (D_d), a proxy for prey availability, was calculated from:

$$D_d = \frac{100\,N}{3600\,t\,W\,H\,V}$$

where N is the total number of invertebrates in a sample, T the number of hours the net sampled, W is the width of the net, H is water depth inside the net and V is the average flow velocity. Drift density is therefore standardized as a function of time and flow and corresponds to the number in invertebrates per cubic meter (Mookerji *et al.*, 2004; Hansen & Closs, 2009). Family taxa richness was expressed as the number of taxa groups present in a sample and relative proportion of EPT and Chironomids was calculated for each sample to characterize the composition of the drift.

Audio files were subsequently analyzed to determine, for each observed individual, the percentage of time associated with each behavior type as well as the proportion of drift versus benthic forays. Foraging behaviour metrics were calculated based on the percentage of time spent feeding, the ratio of drift to benthic forays and the total number of forays over time (Nislow *et al.*, 1998).

Eleven potential explanatory variables for foraging behavior were incorporated into a multiple regression model: julian date, *D. geminata* percent cover, water depth, flow velocity, mean substrate B-axis, water temperature, foray rate, drift density, drift taxa richness, drift %EPT, and drift %Chironomid.

9.3 Results

9.3.1 Drift composition and density

A total of 7 814 individuals were identified in the drift samples, representing 15 different macroinvertebrate orders and thirty-two families, the majority of which being known to constitute potential prey items for JAS (Folt & Parrish, 1994; Keeley & Grant, 1997; Mookerji *et al.*, 2004). Overall, the composition of the drift was dominated by Dipterans (47%), mainly driven by small-bodied Chironomids, and by EPT taxa (18%). The dominance of Chironomids over EPT remained true at all sampled sites. The results of a correlation analysis showed that *D. geminata* percent cover was not significantly related to either drift density ($p = 0.784$), family taxa richness ($p = 0.674$), %Chironomids ($p = 0.309$) or %EPT ($p = 0.799$).

9.3.2 Foraging behaviour

A Spearman rank correlation analysis was used to identify the strongest explanatory variables for foraging behaviour. Regarding the data for the second sampling effort carried out in late summer, there were no significant correlations. Therefore, we excluded this data from the linear regression model. Hence, for the first sampling effort, a Spearman correlation matrix was used and ranks were compared to identify statistically significant ($p \leq 0.05$) correlations between the eleven measured parameters to preselect the explanatory variables for the foraging behavior of 49 JAS (Table 9.4). Foray rate was similar across sites and was not significantly correlated with drift density or flow velocity. JAS that make greater proportions of benthic forays tend to have lower foray rates.

A multiple linear regression model was applied stepwise forward and backwards by eliminating non-significant variables. The results demonstrate clearly that in *D. geminata*-free sites, drift feeding is the dominant behaviour whereas with increasing *D. geminata* percent cover, JAS make higher proportions of benthic forays ($p < 0.001$) (Figure 9.3).

Table 9.4 **P-values of Spearman rank correlations for each measured variable. Significant correlations are in bold**

	Julian Date	Didymo Percent Cover	Depth (cm)	Flow Vx (cm/s)	Mean Axe B	Water temp	%Benthic Foray	Foray rate (# foray/min)	Drift density	Drift taxa richness	Drift % EPT	Drift % Chironomid
Julian Date	1,00	0,41	0,06	0,56	0,01	0,36	0,75	0,24	0,03	0,07	0,00	0,01
Didymo Percent Cover	0,41	1,00	0,25	0,18	0,00	0,32	0,00	0,02	0,23	0,67	0,64	0,52
Depth (cm)	0,06	0,25	1,00	0,60	0,23	0,01	0,04	0,89	0,38	0,11	0,01	0,00
Flow Vx (cm/s)	0,56	0,18	0,60	1,00	0,34	0,31	0,03	0,26	0,07	0,97	0,34	0,57
Mean Axe B	0,01	0,00	0,23	0,34	1,00	0,01	0,08	0,22	0,04	0,16	0,52	0,31
Water temp	0,36	0,32	0,01	0,31	0,01	1,00	0,47	0,38	0,97	0,00	0,72	0,05
%Benthic Foray	0,75	**0,00**	**0,04**	**0,03**	0,08	0,47	1,00	0,00	**0,01**	0,54	0,34	0,64
Foray rate (# foray/min)	0,24	0,02	0,89	0,26	0,22	0,38	0,00	1,00	0,75	0,92	0,44	0,50
Drift density	0,03	0,23	0,38	0,07	0,04	0,97	0,01	0,75	1,00	0,00	0,00	0,00
Drift taxa richness	0,07	0,67	0,11	0,97	0,16	0,00	0,54	0,92	0,00	1,00	0,00	0,00
Drift %EPT	0,00	0,64	0,01	0,34	0,52	0,72	0,34	0,44	0,00	0,00	1,00	0,91
Drift % Chironomid	0,01	0,52	0,00	0,57	0,31	0,05	0,64	0,50	0,00	0,00	0,91	1,00

Within the forward stepwise regression model, this first linear regression, incorporating *D. geminata* percent cover as the only explanatory variable yielded an adjusted $R^2 = 0.49$ and corresponding RMSE of 19,00 and AIC of 429,72 (Figure 9.4 - violet).

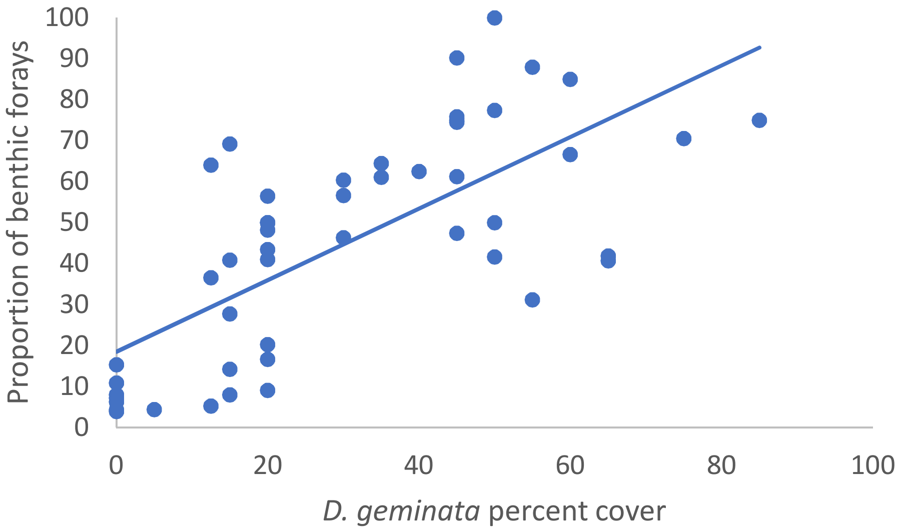

Figure 9.3 **Linear regression of the proportion of benthic forays compared to drift forays in response to increasing *D. geminata* percent cover**

The second linear regression included both *D. geminata* percent cover and Invertebrate drift density as explanatory variables. This model yielded an improved prediction with an adjusted $R^2 = 0.57$ with an RMSE of 17.94 and AIC of 423,76 (Figure 9.4 – green). The third linear regression, incorporated flow as the third explanatory variable resulting in a slightly improved regression model with an adjusted $R^2 = 0.60$ with an RMSE of 16.53 and AIC of 420,7 (Figure 9.4 – red). Depth, although identified as a statistically significant correlation with foraging behavior (Table 9.4), the linear regression model was not significantly improved with this variable and was therefore excluded. For all models, residuals were verified and validated for randomness. The resulting equation is that the observed percent benthic foray proportion is a function of *D. geminata* percent cover, drift density and flow ($p < 0.001$). Benthic foray proportion is negatively correlated with Drift Density.

% Benthic foray = 15.83 + *Dg* percent cover (0.86) - Drift Density (0.51) + flow (0.38)

The stepwise forward models are visually compared in Figure 9.3 where the observed foraging behavior (Blue) is compared to the three forward stepwise models.

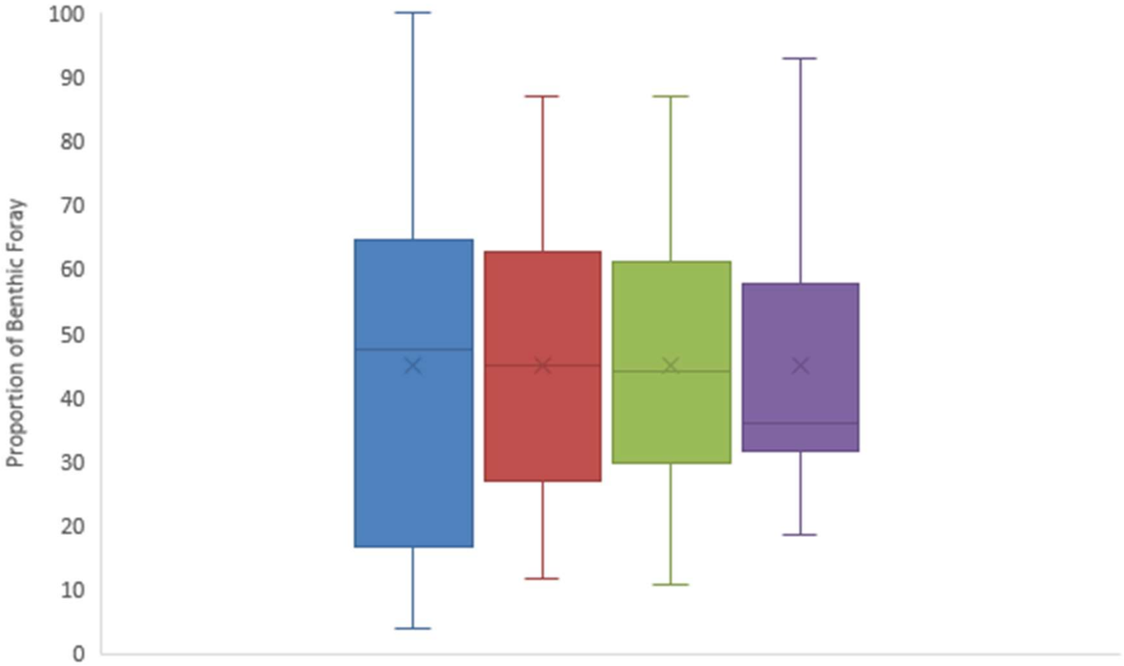

Figure 9.4 **Boxplot of the observed foraging behavior data (blue) compared to the foraging behaviors predicted by the various regression models. The violet model incorporates *D. geminata* percent cover as the only explanatory variable whereas the green model incorporates both *D. geminata* cover and flow. The best fitted model incorporates three explanatory variables: *D. geminata* percent cover, flow and invertebrate drift density (red).**

The resulting model (adjusted $R^2 = 0.60$; RMSE = 16.53; AIC = 420.7) well predicts the foraging behavior but does both under and overestimate the percent benthic foray of some individual JAS (Figure 9.5). No apparent variable was found to drive this discrepancy, although incorporating benthic prey density may improve the model performance.

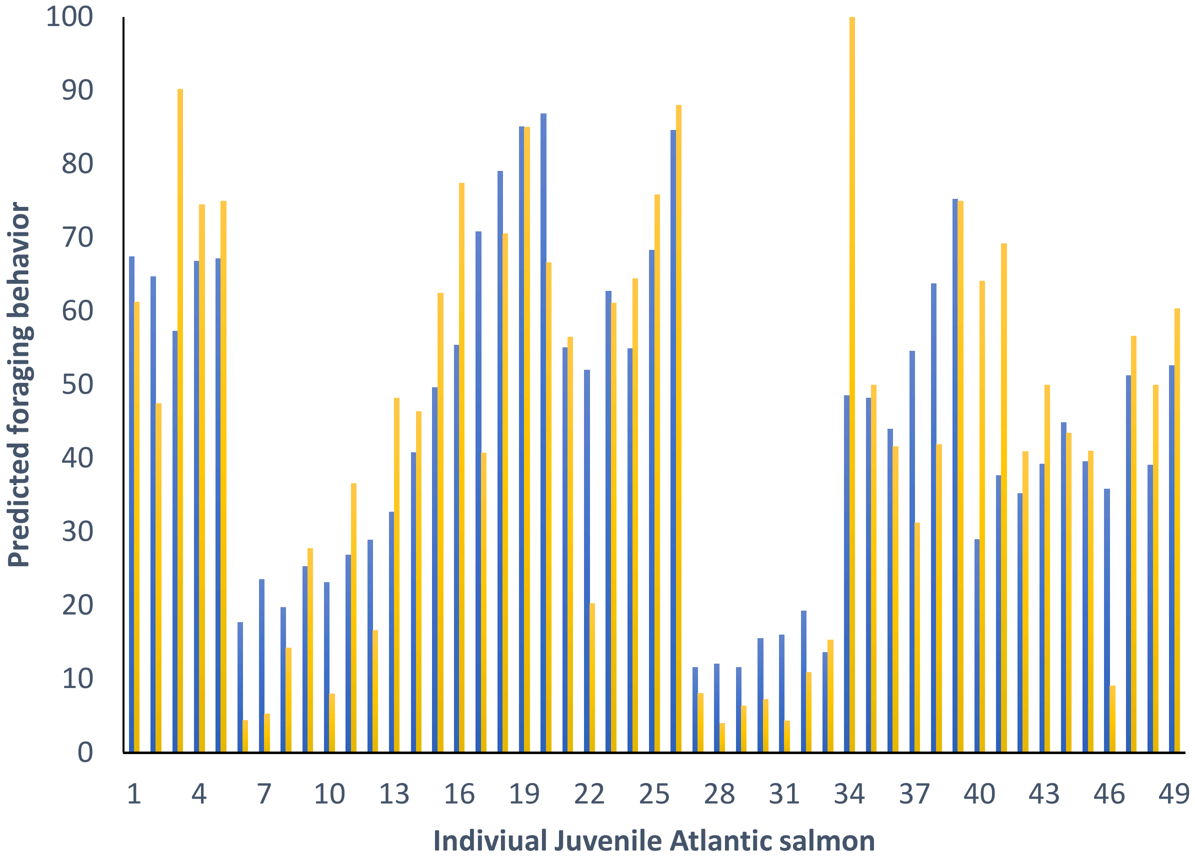

Figure 9.5 **Resulting model fit of the predicted foray proportion (blue) in comparison with the observed foraging behavior data (yellow)**

9.4 Discussion

Our initial hypothesis was that because JAS tend to predominately make drift forays (Keeley & Grant, 1995) and adopt benthic foraging behavior only when invertebrate drift is limited (Nislow *et al.*, 1998), we presumed that JAS were responding to limited drift densities caused by *D. geminata* mats. However, our results show that *D. geminata* percent cover does not drive drifting prey dynamics in terms of abundance or proportion nor does it limit the entrainment of invertebrates in the Patapedia River as no significant correlation was found between these two variables. There was a great variability in drift densities between sites regardless of *D. geminata* cover. Drift samples alone therefore cannot yield sufficient support to highlight the mechanisms under which *D. geminata* alters prey location and production.

Foray rates which are often used as a proxy for prey availability (Nislow *et al.*, 1998), were not correlated with invertebrate drift density. Our behavioral analysis clearly demonstrates that JAS adjust their feeding strategy in response to habitat change, in this case, primarily in response to *D. geminata* percent cover, whereas flow and drift density had minor influence.

The shift in foraging strategies, from drift to benthic with increasing algal mat accrual, may be mainly driven by the increase in benthic prey densities. In fact, previous work conducted on the Matapedia River, an adjacent river stem to the Patapedia River, revealed that *D. geminata* mats increased benthic invertebrate densities by four to five-fold (Gillis & Chalifour, 2010). Benthic prey availability analyses should therefore be completed to fully understand the mechanisms by which *D. geminata* mat presence and severity may alter prey densities, location and drift propensity. We suspect that incorporating benthic invertebrate density data and drift propensity metrics as explanatory variables would improve the foraging behaviour model.

This is the first study to assess the impact of *D. geminata* mats on juvenile Atlantic salmon. Behavioural plasticity and foraging behaviour need to be accounted for to fully disentangle direct and indirect effects of this alga on salmonids. Shifts in foray type and rate can further explain the mechanisms by which salmonids respond to increasing benthic biomass accrual in lotic environments. Future bioenergetic models used in assessing the impact of *D. geminata* on growth and condition of salmonids will need to incorporate our findings.

CHAPITRE 10

ASSESSMENT OF SEASONAL DIETARY SHIFTS OF JUVENILE ATLANTIC SALMON (*SALMO SALAR*) DRIVEN BY *DIDYMOSPHENIA GEMINATA* MATS USING A STABLE ISOTOPE ANALYSIS APPROACH

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Abstract

Didymosphenia geminata has recently emerged worldwide as a nuisance alga. This mat-forming diatom exudes stalk material creating thick benthic mats that have been shown to affect lower trophic levels. Limited research has attempted to identify the effects of *D. geminata* presence on higher trophic levels such as salmonids. Here we use stable isotope analysis (SIA) to assess if dietary shifts occurred in juvenile Atlantic salmon (JAS) sampled in two contrasting sites, one where mats were absent and one where mats dominated the benthic habitat covering 90% of the river substrate with a mean thickness of 21 mm, of the Northwest Upsalquitch River (New Brunswick, Canada). Secondly, we assessed the impact of *D. geminata* mat presence on trophic niche width as well as size-at-age of JAS. Seasonal dietary shifts towards carbon depleted prey were observed in both sites regardless of the presence-absence of *D. geminata* mats, but prey source reliance differed significantly. In the un-impacted sites, JAS consumed a greater proportion of scrapers (Ephemeroptera) whereas in the impacted site, JAS consumed greater proportion of chironomids (collectors). Lower values of Total Area (TA), a Layman metric describing niche width, indicates that in presence of *D. geminata* mats, trophic niche size and diversity were negatively affected. Conversely, invertebrates within the didymo matrix have a broader niche width, highlighting diverse resource use within the complex biofilm. However, JAS C:N ratios and condition factors were not significantly different between sites, indicating compensatory mechanisms for optimal foraging and growth. Further research is warranted to truly disentangle the impact of *D. geminata* on salmonids and to identify the mechanisms of disruption.

Keywords: Seasonal dietary shift, juvenile Atlantic salmon, *Didymosphenia geminata,* FGG, mixing model, stable isotope analysis

10.1 Introduction

Didymosphenia geminata Lyngbye (M. Schmidt) is a mat-forming diatom that can produce copious amounts of stalk material in oligotrophic lotic ecosystems. In recent years, increased prevalence of nuisance growths has been reported in rivers and streams around the globe (Bothwell *et al.*, 2014). Research efforts have mainly focused on the causes of this emergence and recent work has verified impacts of mats on diatom assemblages and macroinvertebrate abundance and community structure (Gillis & Chalifour, 2010; Kilroy *et al.*, 2010; James *et al.*, 2011; Anderson *et al.*, 2014; Gillis & Lavoie, 2014), but rarely have they attempted to identify the underlying mechanisms by which established *D. geminata* mats alter trophic dynamics (Reid & Torres, 2014). Recent research conducted in Sierra Nevada indicated that *D. geminata* mats significantly altered the availability of benthic resources to tadpoles and consequently decreased their growth rates (Furey *et al.*, 2014).

In terms of the impacts of *D. geminata* mats on fish, previous studies showed no link between *D. geminata* prevalence and decreased anadromous salmonid production in western Canada, Norway and Iceland (Bothwell *et al.*, 2008; Jonsson *et al.*, 2008; Lindstrom & Skulberg, 2008). Earlier bioenergetics modelling efforts, based on drifting prey availability, also concluded that *D. geminata* may not have a negative impact on foraging and growth of drift-feeding salmonids (Shearer *et al.*, 2007; James *et al.*, 2011). However, Jellyman and Harding (2016) found a direct negative effect on fish biomass in New Zealand rivers.

In eastern Canada, earlier work showed that the presence of didymo caused significant changes in macroinvertebrate community structure and abundance by decreasing proportions of EPT (Ephemeroptera, Plecoptera, Trichoptera) and increasing proportions of chironomids (Gillis & Chalifour, 2010). For salmonids, such shifts in these food resources could potentially alter the availability and quality of prey and thus have considerable effects on growth and condition (Gillis & Chalifour, 2010; Anderson *et al.*, 2014; James & Chipps, 2016). Two recent publications presented shifts in trout diet in response to *D. geminata* mats using stomach content analysis: James and Chipps (2016) found that gut contents were representative of the macrobenthic community composition whereas Jellyman and Harding (2016) found that trout maintained prey selection for EPT taxa in various biomass levels of *D. geminata.*

Because gut contents show the relative consumption of different prey species within a recent and short timeframe, it does not integrate dietary shifts in response to a changing environment (Grey, 2001; Sakano *et al.*, 2005; Dixon *et al.*, 2012). However, Carbon and Nitrogen stable isotope ratios respectively inform on dietary sources and trophic position, hence helping identify putative prey reliance in contrasting habitats (DeNiro & Epstein, 1979; Peterson & Fry, 1987; Grey, 2001). Because tissue types differ in terms of turnover rates, they can help inform on various aspects of dietary shifts (Yeakel *et al.*, 2016). Tissues with rapid isotopic turnover rates, such as liver, reflect a more recent diet than tissues with slower turnover rates, such as muscle, and depends essentially on growth (Tieszen *et al.*, 1983; Perga & Gerdeaux, 2005; Thomas & Crowther, 2015). In fish, differences in liver and muscle signatures are useful to identify seasonal shifts in consumed prey resources (Haas *et al.*, 2009; Heady & Moore, 2013). Mixing models can then be used to determine the potential relative contribution of different prey items to the consumer's diet (Grey, 2001; Jackson *et al.*, 2012).

Thus, since the base of the food resource is impaired in the presence of *D. geminata* (Kilroy *et al.*, 2009; Gillis & Chalifour, 2010; James *et al.*, 2010), it is likely that the isotope ratios of juvenile salmon are altered due to potential diet shifts. Isotopic ratios of juvenile salmon tissue reflect their habitat use in relation to their foraging strategies and inform on their putative energy sources (Cunjak *et al.*, 2005; Kennedy *et al.*, 2005; Rasmussen *et al.*, 2007; Jackson *et al.*, 2012). Further, lipid is a carbon based compound but contains practically no nitrogen, hence elemental carbon to nitrogen (C:N) ratios can be used to infer lipid content of a consumer and assess diet quality (McCutchan *et al.*, 2003; Logan *et al.*, 2008). This type of integrated analysis therefore offers an interesting opportunity to describe diets of juvenile Atlantic salmon associated with the presence and absence of *D. geminata* growths.

The main objective of this study was to assess how the presence of dense fibrous mats impacts the structure of the food web and energy sources for higher trophic levels such as juvenile Atlantic salmon. To identify potential dietary shifts, we first tested whether isotopic signatures of muscle and liver tissues of juvenile Atlantic salmon fry and parr were different between impacted and non-impacted sites. Then, we quantified the food web structure and trophic niche width of these contrasting sites. Finally, we compared the condition factors of fry and parr between sites.

10.2 Methods

10.2.1 Study Area

The study was conducted on the Northwest Upsalquitch River (New Brunswick, Canada) (Figure 10.1), a tributary of the Restigouche River, where persistent to occasional *D. geminata* mats have been observed since 2007. Two sampling sites were selected for the study, one where *D. geminata* was absent and one where it covered 90% of the bed surface (Figure 10.2). Albeit their difference in *D. geminata* coverage, the two sites were similar in terms of depth, substrate and flow velocity, conductivity and riparian canopy cover (Table 10.1).

Table 10.1 Site characteristics of the sampled river reaches

Site	Max Depth (cm)	Habitat type	Conductivity (µS)	Dominate substrate type	Overhanging vegetation	*Dg* % cover
9 mile	60	Run	113,8	Cobble	None	0
Craven	72	Run	122,5	Cobble	None	90

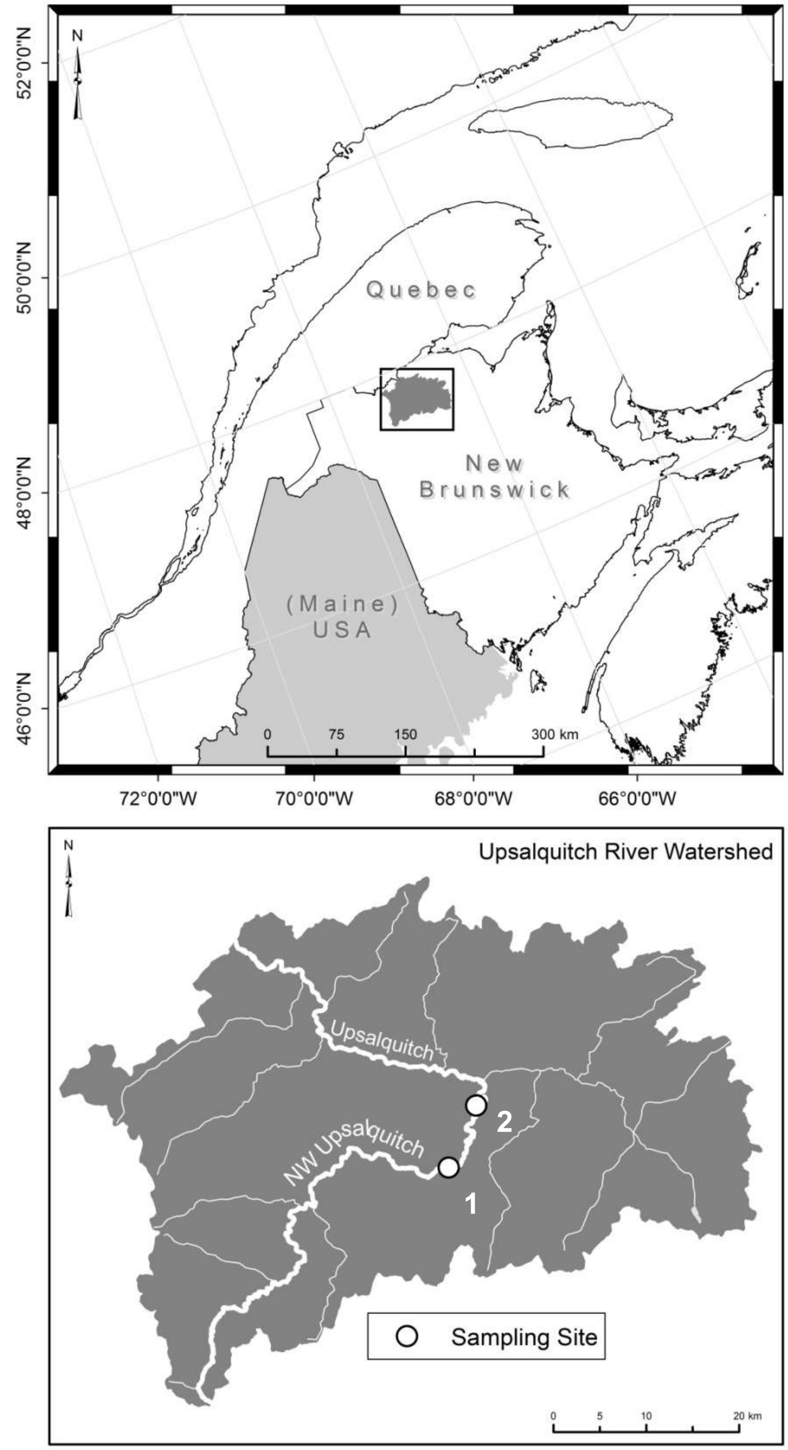


Figure 10.1 Sampling sites location in the Northwest Upsalquitch River, tributary of the Upsalquitch River. This Upsalquitch River watershed is a sub-catchment of the Restigouche River watershed in Northern New-Brunswick. Site 1 (9 mile) is the upstream control site without *D. geminata* presence whereas site 2 (Craven) is the downstream impacted site with persistent *D. geminata* mats.

10.2.2 Standing Crop Index (SCI)

At each site, a Standing Crop Index (SCI) of *D. geminata* severity was estimated using the method of Kilroy and Bothwell (2012) where percent cover is multiplied by the thickness of the mat (mm). At the non-impacted site, 9-mile, SCI was 0 whereas Craven's Gulch, the impacted site, SCI was estimated at 1890 (90% cover with a mean mat thickness of 21mm).

Figure 10.2 SCI contrast between sites. Left panel is the unimpacted site (9 mile) and the right panel is the *D. geminata* impacted site with thick benthic mats.

10.2.3 Prey and consumer collection

At each site, two components of the food web were sampled: benthic macroinvertebrates and juvenile Atlantic salmon. In order to examine possible temporal shifts in isotopic ratios, composite samples of benthic macroinvertebrates were sampled on two occasions at the same sites, once in late August and once in late September 2011, using a Surber D-net (Pelletier & Moisan, 2006). During the September sampling, two age classes of wild juvenile Atlantic salmon were also sampled, 12 fry (≤ 60 mm) and 12 parr (≥ 61 mm) at each site with a Smith-Root LR-24 electrofisher.

10.2.4 Sample processing

All samples were frozen within two hours of sampling. In the laboratory, samples were thawed and benthic macroinvertebrates were sorted and identified to family-level (Merritt & Cummins, 2008). Taxa were pooled at order-level resolution as obligate functional feeding groups (FFG) based on Merritt and Cummins (2006). Sample composites comprised of at least 10 individuals were prepared (Table 10.2). All orders were present in both sites and all of which are considered potential prey for juvenile Atlantic salmon (Keeley & Grant, 1997).

Table 10.2 Invertebrate taxa groupings for stable isotope analysis of prey sources

Order	Representative families	Functional Feeding Group
Plecoptera	Perlidae	Predator
Odonata	Anisoptera	Predator
Diptera	Chironomidae	Collector
Ephemeroptera	Heptageniidae, Ephemerellidae	Scraper

White dorsal muscle was dissected from each individual Atlantic salmon. The liver of each individual was extracted, but those of salmon fry of a same site were combined into a composite sample in order to achieve sufficient sample mass for isotope analysis. In total, 17 benthic macroinvertebrate (BMI) composite samples and 78 fish tissue samples were dried at 60°C for a period of 24 hours, grinded into a fine homogeneous powder, and stored in Eppendorf vials. Samples were then shipped and analysed for carbon and nitrogen. Sample weights and stable isotope analysis were conducted by SINLAB, University of New Brunswick.

10.2.5 Mathematical normalization

C:N ratios are commonly used to infer on lipid contents of fish (McCutchan *et al.*, 2003; Logan *et al.*, 2008). Because carbon fractionation in high lipid tissues can create bias in diet interpretation from mixing models results when C:N ratios of consumers are above 3.5, we conducted a mathematical lipid normalization (Skinner *et al.*, 2016). δ^{13}C values of both tissue types from fry and parr were corrected using Equation 1 for the lipid normalization model (Kiljunen *et al.*, 2006) with Equation 2 (Post *et al.*, 2007) for percent lipid (L) calculations of salmonids where:

$$\delta^{13}C' = \delta^{13}C + D \times \left(I + \frac{3.90}{1 + 287/L}\right) \qquad (1)$$

Where D = 7.018 (the isotopic difference between protein and lipid), constant I = 0.048 and

$$L = -20.54 + 7.24 \times C{:}N \qquad (2)$$

10.2.6 Data analysis

10.2.6.1 Effect of D. geminata on juvenile Atlantic salmon resource use

Mixing models were created with the MixSIAR package (Stock & Semmens, 2013) in R (version 3.2.3). A mixing model was generated for each site to identify likely prey items consumed by juvenile Atlantic salmon. Because fry and parr isotopic signatures between age classes did not significantly differ within sites, they were pooled for a same site. Mixture data for consumers was organized by tissue type and set as a random effect. MCMC length was set to normal to enable convergence. For prey items, where *n isotopes +1* correspond to the number of sources to input into the mixing model, all invertebrate data were assigned to three obligate FFGs (predators, scrapers and collectors) as end members of the river food web and entered as raw data. Diet-tissue discrimination factors to account for trophic fractionation, also known as trophic enrichment factors (TEFs), were obtained from existing published values in McCutchan *et al.* (2003) and Heady and Moore (2013). Fractionation values used for sources were $\delta^{13}C$: 1.3± 0.3 and $\delta^{15}N$: 2.9 ±0.3.

10.2.6.2 Food web structure and diversity

The Stable Isotope Bayesian Ellipses in R (SIBER) package (Jackson *et al.*, 2011) was used to estimate community-level Layman metrics (Layman *et al.*, 2007) allowing the comparison of isotopic niches between the two sampling sites. Input data was organized into two communities (CRAVEN and 9 mile) in which each had three groups: Atlantic salmon fry, Atlantic salmon parr, and invertebrates.

Here, we provide a brief description of each Layman metric. The $\delta^{15}N$ Range (NR), corresponds to the trophic length of the food web and the difference between the maximum and minimum values of $\delta^{15}N$. The $\delta^{13}C$ range (CR) is the difference between the minimum and maximum values of $\delta^{13}C$ and constitutes a proxy for estimating the diversity of basal resources. Total area (TA) corresponds to the convex hull area incorporating all the species within the bi-plot space. This metric is also a measure of niche width (Jackson *et al.*, 2012). Mean distance to centroid (CD) metric also informs on the trophic diversity within the food web. Mean nearest neighbor distance (MNND) describes the overall density and clustering of species whereas the standard deviation of nearest neighbor distance (SDNND) is a measure of the spatial evenness of the species packing.

10.2.6.3 Condition factor of juvenile Atlantic salmon

Condition factors (K) were estimated with Gibson (1993) equation, where W is the weight in grams and FL corresponds to the fork length in millimetres.

$$K = \frac{W \times 10^2}{FL^3}$$

10.3 Results

D. geminata prevalence reports from July and August indicated that the upstream site, 9 mile, did not present any mat accrual, whereas at the downstream site, Craven's Gulch had persistent 90% mat cover during the same period.

10.3.1 Stable isotopes signatures

10.3.1.1 Macroinvertebrate community

Comparison of the two sampled sites show that pooled $\delta^{13}C$ invertebrate signatures tend to be less negative in the impacted site (Craven) than in the unimpacted site (9 mile) except for Ephemeroptera (Figure 10.3). In the *D. geminata* affected site, Trichoptera have similar $\delta^{13}C$ signatures to Chironomids whereas these two orders contrast in terms of $\delta^{13}C$ values in the *D. geminata* free site. Predatory invertebrates (Odonates and Plecoptera) have similar isotopic signatures in both sites.

10.3.1.2 Juvenile Atlantic salmon

Salmon $\delta^{13}C$ values in 9 mile are located at the center of the prey continuum, whereas $\delta^{13}C$ values of salmon in the presence of *D. geminata* are less negative similar to prey items such as Chironomids (Figure 10.3).

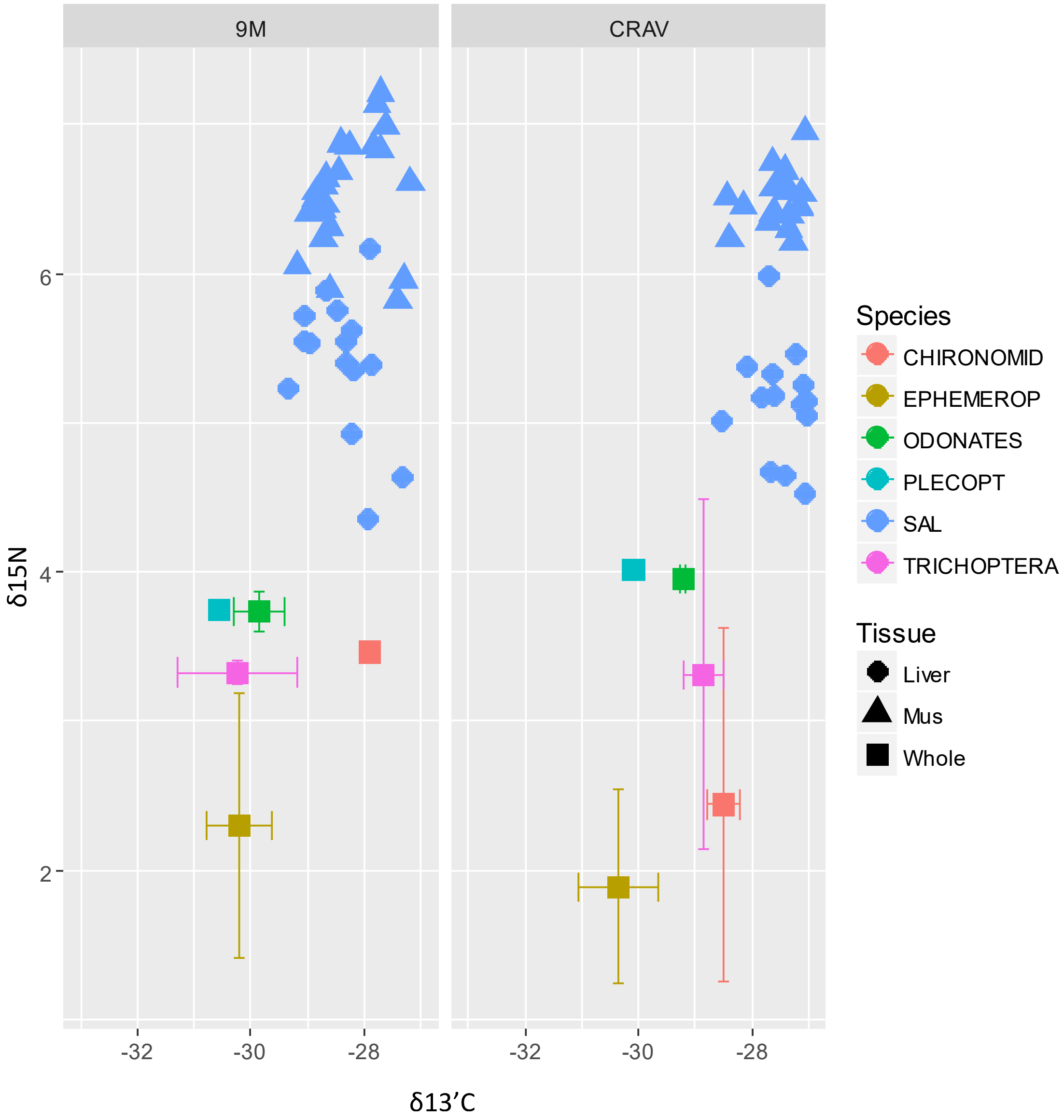


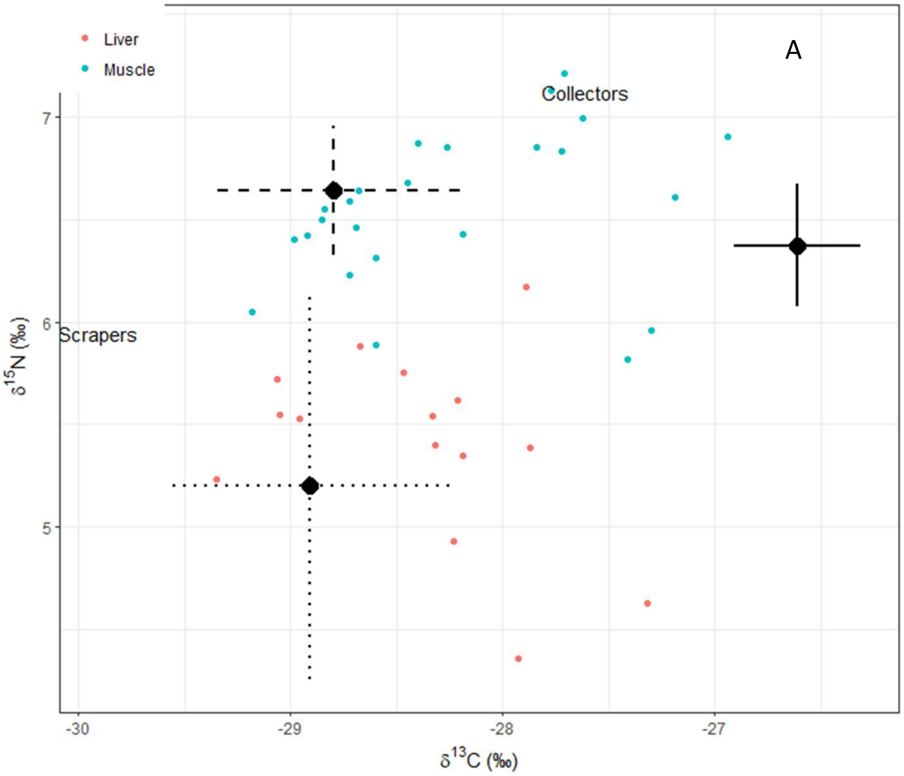
Figure 10.3 **Biplot of stable isotope ratio data for all sample types in both sites. 9M refers to the un-impacted 9-mile site and CRAV refers to the *D. geminata* impacted site. Each species is presented with a different color and each tissue type with a different shape.**

Paired *t*-tests were used to statistically compare JAS isotopic values of lipid-corrected δ^{13}C in both sites (Table 10.3). All tissue types and age class comparisons were statistically different except between fry muscle and parr muscle δ^{13}’C ratios in the *D. geminata* impacted site (Craven) where resource use, as inferred from their carbon signatures, may be similar between fry and parr life stages.

Table 10.3 **Results of paired *t*-tests comparing lipid-corrected carbon isotope ($\delta^{13'}$C) ratios for each cohort (age class) and tissue type within and between sampling sites**

Paired t-tests	*T*	d.f.	Significance	Mean difference
Within sites				
9M: Fry muscle vs. Parr muscle	-4.06	11	0.002	-0.82 ± 0.70
Craven: Fry muscle vs. Parr muscle	-1.09	11	0.301	0.22 ± 0.71
Between sites				
Fry liver: 9M vs. Craven	-4.67	2	0.043	-0.45 ± 0.17
Fry Muscle: 9M vs. Craven	-3.96	11	0.002	-0.61 ± 0.53
Parr liver: 9M vs. Craven	-7.99	11	< 0.001	-1.11 ± 0.48
Parr Muscle: 9M vs. Craven	-5.67	11	< 0.001	-1.21 ± 0.74

When comparing samples from the impacted and non-impacted sites, 9-mile isotope ratios were always more carbon enriched whereas the Craven samples were carbon depleted by ~1‰ (Figure 10.4). The position of consumers in δ-space appears mostly driven by differences in resource use. In Craven, JAS values for both tissue types are significantly less negative in comparison to tissue signatures from 9-mile (Table 10.3).



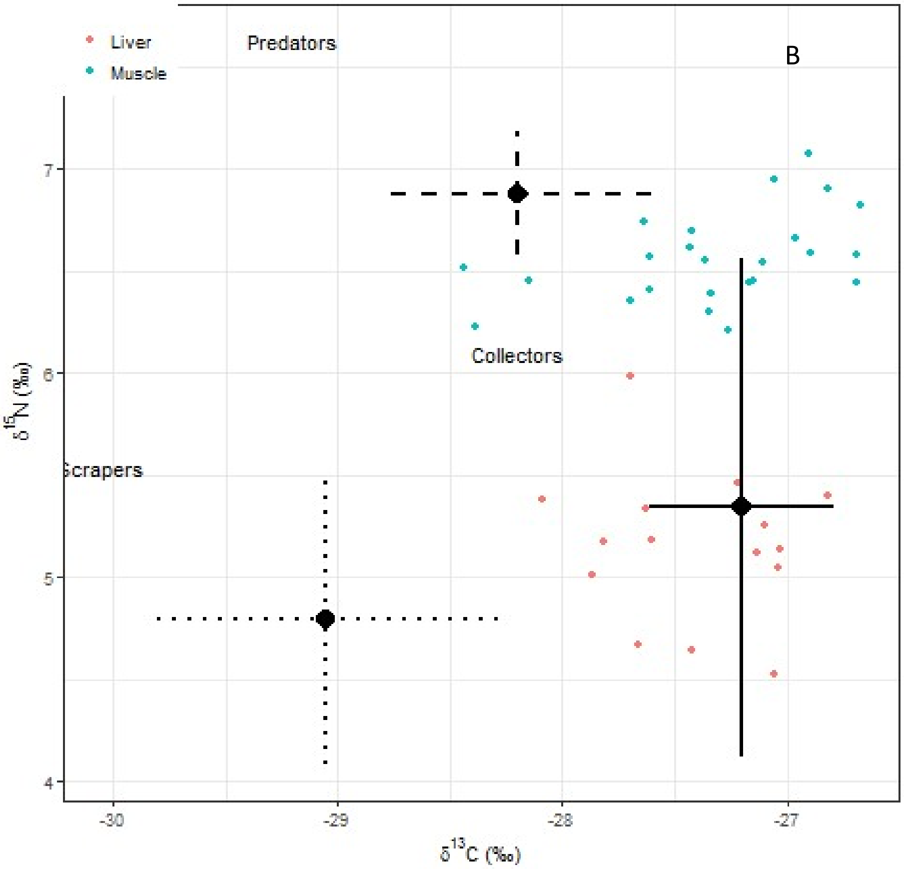


Figure 10.4 Isospace plot of prey sources and consumers for 9 mile (A) and Craven (B)

The median contribution of each functional feeding group to the diet of juvenile Atlantic salmon in each site is presented in Table 10.4. Recent median diet proportions, as depicted by liver tissues, are 74.7% scraper, 2.8% collector and 7.7% predator for JAS in the non-impacted site, and 1.9% scraper, 89.1% collector, and 1.0% predator for those in the impacted site. As for the integrated seasonal diet, as depicted by muscle tissues, median diet proportions are 0.3% scraper, 1.2% collector, and 93.9% predator for JAS in the non-impacted site, and 0.9% scraper, 15.9% collector, and 80.9% predator for those in the impacted site. The mixSIAR model confirms seasonal shifts of JAS prey reliance from invertebrate predators in both sites towards scrapers in the un-impacted site but towards collectors in the impacted site.

Table 10.4 Median integrated diet contributions of each FFG to consumers (pooled fry and parr). Likely proportions are presented by tissue type where liver would be considered as recent diet (2-3 weeks) and muscle as seasonal diet (3-4 months) with 95% credibility intervals (CI) for each prey source. Prey reliance CI's with no zero values are in bold.

	9 mile		**Craven**	
Source	*Liver*	*Muscle*	*Liver*	*Muscle*
Scraper	26.9 ≤ **74.7** ≤ 100	0 ≤ 0.3 ≤ 15.6	0 ≤ 1.9 ≤ 62.3	0 ≤ 0.9 ≤ 35.0
Collector	0 ≤ 2.8 ≤ 39.6	0 ≤ 1.2 ≤ 37.4	14.8 ≤ **89.1** ≤ 100	0 ≤ 15.9 ≤ 39.9
Predator	0 ≤ 7.7 ≤ 69.9	59.9 ≤ **93.9** ≤ 100	0 ≤ 1.0 ≤ 56.2	44.0 ≤ **80.9** ≤ 92.7

10.3.2 Food web structure and diversity

The δ^{15}N range and CD metrics were slightly higher at the Craven site but consumers are considered to belong to the same trophic level in both sites as their mean distance to centroid (CD) is an averaged measure of trophic diversity among consumers (Jackson *et al.* 2011). $\delta^{13'}$C range was greater in 9-mile indicating a broader diversity of diet sources in the un-impacted site (Table 10.5).

Table 10.5 Community level Layman metrics extracted from SIBER for comparison between sites.

Metric	**9-mile**	**Craven**
δ^{15}N Range (NR)	3.20	3.39
$\delta^{13'}$C Range (CR)	2.18	1.98
Convex Hull Area (TA)	1.15	0.46
Mean distance to centroid (CD)	1.62	1.71
MNND	1.67	1.44
SDNND	1.44	2.07

Further, in the presence of *D. geminata* mats, Convex Hull Area (TA) is lower than in the *D. geminata* free site, indicating that trophic niche width as well as niche diversity is negatively affected by the presence of *D. geminata* mats (Table 10.5; Figure 10.5). Additionally, Layman metrics CR, TA and MNND are higher in the unimpacted site and SDNND lower, indicating an even reliance on greater prey diversity in comparison to the impacted site.

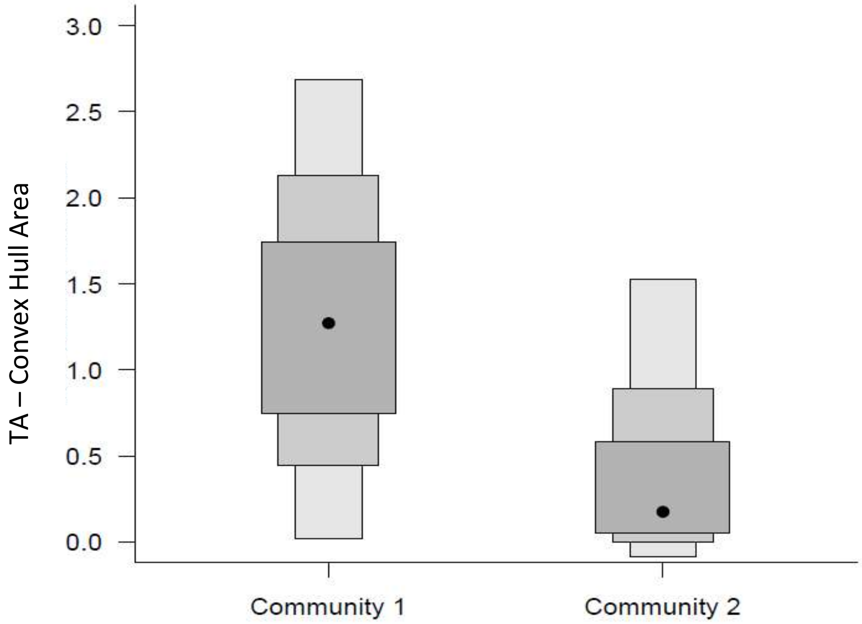


Figure 10.5 Convex Hull Area (TA) of both communities (community 1: 9-mile; community 2: Craven).

As for population level metrics, Standard Ellipse Area (SEAc) is relatively similar between sites for parr (Table 10.6). Contrastingly, SEAc and TA values for fry are significantly lower in the *D. geminata* affected site (p = 0.018). Conversely, trophic metrics of invertebrate sources are significantly higher in Craven compared to 9-mile (p = 0.012) indicating a very broad niche width and diverse resource use by various FFGs within the complex biofilm (Table 10.6).

Table 10.6 Layman metrics extracted from SIBER for each group (source and consumers) within each sampling site

	9 mile fry	Craven fry	9 mile parr	Craven parr	9 mile Inverts	Craven Inverts
TA	1.50	0.47	0.66	0.65	0.31	2.15
SEA	0.77	0.21	0.31	0.30	0.40	1.85
SEAc	0.85	0.23	0.34	0.34	0.59	2.47

10.3.3 Condition factor of juvenile Atlantic salmon

Condition factor (K) of juvenile Atlantic salmon was measured for both life stages (Table 10.7). While Craven JAS have a slightly higher condition factor than 9-mile JAS, there is no statistical difference in the condition of fish between sites. C:N ratios were also not significantly different between sites for both tissue types (Paired *t*-test > 0.05). We also found no significant correlation between K and recent diet as reflected by the δ^{13}’C liver signatures.

Table 10.7 Size and condition of fry and parr in each sampling site. Twelve fry and twelve parr were sampled

Site	Mean values for fry				Mean values for parr			
	Fork length (mm)	**Weight (g)**	**Condition factor (K)**	**C:N**	**Fork length (mm)**	**Weight (g)**	**Condition factor (K)**	**C:N**
9-mile	54	1.53	0.96	3.54	91	7.29	0.96	3.27
Craven	57	1.86	1.01	3.50	83	5.73	1.01	3.18

10.4 Discussion

10.4.1 Shifting prey resources

Our results show insights into the dietary shifts and response of invertebrates and JAS to *D. geminata* mats. Due to major habitat structure differences between the unimpacted and impacted sites with regards to mat accrual and biomass, we hypothesized that there would be differences in prey sources and JAS isotopic ratios. Our study demonstrates that JAS $\delta^{13}C$ diets are depleted in presence of *D. geminata* and that this trend is strongest when comparing liver signatures, which would indicate that JAS consumed less negative prey in the presence of *D. geminata*.

When comparing isotopic ratios of invertebrate taxa in the biplot between sites, Trichoptera were less negative within the impacted site and presented similar carbon signatures to Chironomids. Since Chironomids consume algae and detritus, and Trichoptera consume detritus and Chironomids, we suggest that the increased biofilm complexity offers Chironomids refuge from predatory invertebrates. Algal mats are known to provide a predatory refuge for Chironomids (Power, 1990) and many studies have reported a profusion of Chironomids within the *D. geminata* mat matrix (Larson & Carreiro, 2007; Kilroy *et al.*, 2009; Gillis & Chalifour, 2010; James *et al.*, 2010). Because of this predator avoidance strategy, Trichoptera may have to primarily rely on detritus, thus explaining similar isotopic ratios between Trichoptera and Chironomids within the *D. geminata* impacted site. Validation of this suggestion should be carried out in future experimental studies to elucidate pathways by which *D. geminata* mats impact higher trophic levels.

When comparing muscle tissues within sites, there was a significant difference between JAS age classes for 9-mile whereas in Craven, muscle signatures for fry and parr were similar indicating a similar integrated diet. The similar isotopic signatures between age classes, regardless of mouth gape and preferred prey source, indicates that parr are not exploiting food resources differently than fry but rather consuming smaller and carbon depleted prey items in the *D. geminata* impacted site.

When comparing between sites, $\delta^{13}C$ signatures of liver and muscle were all significantly different. In both sites, seasonal dietary shifts were determined by the contrasting turnover rates of the sampled tissues which highlights changes in dominant prey source over time. In 9-mile, prey reliance shifted from predatory invertebrates to scrapers whereas in the *D. geminata* impacted site, prey reliance shifted from predatory invertebrates to collectors, i.e. chironomids. In both sites, a seasonal shift in dietary sources from predators to smaller prey items was evident. Further, it would be warranted to investigate whether

JAS are actually consuming Chironomids in *D. geminata* impacted sites, or rather, if they are consuming a prey type with similar isotopic ratios such as Trichoptera. James and Chipps (2016) found that brown trout diet composition, determined by gut content analysis, resembled the species composition of benthic samples and diet constituted by a greater proportion of Chironomids than EPT taxa.

Contrasting availability and community structure of the prey base between sites may explain the reliance on different functional feeding groups (FFG) between the unimpacted and impacted sites. *D. geminata* mat accrual is known to skew proportions of invertebrate taxa, where %EPT declines and %Chironomids increase (Kilroy *et al.*, 2009; Gillis & Chalifour, 2010; James *et al.*, 2010) and to decrease diversity (Anderson *et al.*, 2014). Rost (2010) also found that *D. geminata* mat presence reduced scraper densities and where FFG with less specialised feeding behavior, such as burrowing Chironomids, would thrive in the extensive mat cover. This may therefore impact the dominant prey type readily available to foraging salmonids.

10.4.2 Food web structure and diversity

JAS in 9-mile relied more evenly on a diverse prey base than JAS from Craven. Fry, as identified by their lower SEAc and TA values, tend to consume less diverse prey items whereas parr tend to consume smaller prey items in the presence of *D. geminata*. As for invertebrates, they showed the most contrasting trophic differences between sites with a significantly greater niche width and diverse resource use with *D. geminata* presence. Because *D. geminata* mats are dense interwoven stalks that harbour small diatoms, detritus and bacteria (Kilroy *et al.*, 2006; Spaulding & Elwell, 2007; Whitton *et al.*, 2009), we suppose that there is an abundance of diverse resources within the thick matrix of mucilage that invertebrates consume. Future work would be conducted to investigate gut contents of various invertebrate species and their resource use in various levels of *D. geminata* mat severity.

10.4.3 Consequences of prey quality on fish

Based on previous studies where *D. geminata* was shown to increase smaller-bodied taxa with associated lower caloric values and decreased %EPT, we hypothesized that there would be a clear impact of carbon depleted diets on fish condition. However, although we identified some shifts in prey resource use both seasonally and spatially, there were no apparent impact on C:N ratios, a proxy to infer lipid content, or on condition factors (K) of juvenile Atlantic salmon. Regardless of their relative C:N ratios and K factors, parr from Craven have an average weight 2g lower than parr of the same age from site 9-mile indicating that *D. geminata* mats may affect growth rates and size-at-age rather than condition or lipid content.

Future work is warranted to investigate if the quality of prey is affected by *D. geminata* and whether it will impact mean daily weight gain and size-at-age of JAS. Juvenile Atlantic salmon tend to maximise their energetic gain and are behaviourally plastic and may have adjusted their foraging strategy to still select preferable prey as observed by Jellyman and Harding (2016). Foraging behaviour plasticity of JAS in response to increasing mat accrual (Gillis & Bergeron, Chapter 9*)* probably compensated and limited the effects of depleted diets on condition. Gut content analysis may then be helpful to compare benthic and drifting prey availability towards understanding prey resource use in *D. geminata* affected reaches. Future studies should also asses the effects of *D. geminata* mats on intraspecific resource competition and habitat use and selection for juvenile Atlantic salmon.

10.5 Conclusion

Food webs, by their very nature, are complex. The effects of *D. geminata* on trophic dynamics of streams will likely vary with many factors, including the extent of coverage, thickness and duration of mats. This effort helped identify seasonal changes in juvenile Atlantic salmon resources regardless of *D. geminata* mat presence by using two tissue types with differing turnover rates. It also provides the first assessment linking *D. geminata* proliferations impact on juvenile Atlantic salmon diet using stable isotopes and provides some insight into pathways by which *D. geminata* is altering resource use. We suggest that future stable isotope analyses for assessing shifts in trophic pathways, include a greater number of sources and sample size to reduce the confidence intervals in the mixing model output and reduce the putative prey sources overlap.

In New Zealand, Harding and Jellyman (2016) concluded that *D. geminata* has a complex detrimental effect on fish communities. The extent to which *D. geminata* impacts structure and function of lotic food webs will need to be investigated further and will most likely be variable worldwide and dependant on the species composition of the study areas. Food web impact studies are therefore needed in a broad range of environments where *D. geminata* nuisance growths are occasional to severe, while considering the seasonal dynamics of these growths will be key in defining the underlying mechanisms disrupting ecosystem function. As suggested by Rost (2010), it would also be of great value to determine the thresholds of *D. geminata* mat severity for adverse effects in rivers and streams.

Impacts of *D. geminata* on freshwater ecosystems span beyond simple predator-prey relationships, we suggest that future studies use a fatty acid (FA) based approach to asses a broader array of biomarkers to identify the pathways of disruption with fatty acids.

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CHAPITRE 11
MANAGEMENT CHALLENGES OF *DIDYMOSPHENIA GEMINATA*

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At the International Didymo Conference (Providence, Rhode Island, USA, 2013), federal, state and local land managers asked for advice from the international scientific community. Managers need to know how to respond to nuisance growths of *Didymosphenia geminata* (Lyngbye) M. Schmidt. The appropriate management response, however, may depend on particular geographic regions of concern.

In New Zealand, *D. geminata* is considered a "harmful and undesirable pest" (Hammond, 2013) and Biosecurity New Zealand has developed a comprehensive management plan, specific to the island nation. Despite aggressive efforts at containment, beginning in 2004, the diatom spread rapidly to grow in over 140 South Island rivers (Kilroy & Unwin, 2011). Management and public education was further directed at preventing a North Island incursion. Experimental control of nuisance growths was also tested in New Zealand (Arscott, 2008; Shearer *et al.*, 2008) although there is little support for the efficacy of eliminating, or even reducing, this microorganism from a river reach. In Chile, *D. geminata* was detected relatively recently, and the organism has been labeled negatively, as a "plague". Recommendations for management action have largely been based on knowledge gained from New Zealand, specifically by focusing on defensible watersheds, where potential introductions can be tightly controlled (Reid *et al.*, 2012). In Europe and Asia, where nuisance mats have occurred historically, *D. geminata* is considered a native species and there are generally no efforts directed at management (Ellwood & Whitton, 2007). In North America, *D. geminata* has variously been considered native or invasive and there has been no consistent message to managers about how to respond (Root & O'Reilly, 2012). The purpose of this note is to provide a clear recommendation to North American land managers based on the most recent science.

Over the past decade, much of the discussion about impacts caused by *D. geminata* has pivoted on the characterization of the species as native versus invasive. Indeed, historical records document the long-term presence of *D. geminata* throughout the northern circumboreal region (Blanco & Ector, 2009), and reports from the southern hemisphere (in New Zealand, Chile and Argentina) reinforce the assertion that *D. geminata* is a more recent invader (Kilroy & Bothwell, 2011; Cullis *et al.*, 2012; Sastre *et al.*, 2013). Although it is clear that *D. geminata* is transported easily by a variety of vectors, including humans (Kilroy & Unwin, 2011) and aquatic mammals (Leone *et al.*, 2014), as well as by passive dispersal (Lavery *et al.*, 2014), we may be misled by the native/invasive dichotomy. The substantive issue of concern with *D. geminata* is the formation of thick mats of stalk material in streams and rivers, in both native and non-native ranges.

Thick mats of stalk material induce dramatic alteration of aquatic ecosystems, affecting their structure and function (Kilroy *et al.*, 2009; Gillis & Chalifour, 2010; James *et al.*, 2010) and decreasing aesthetic value

(Spaulding & Elwell, 2007; Beville *et al.*, 2012). With increasing cover of benthic mats of *D. geminata,* algal composition shifts to assemblages that are homogenous and lower in diversity (Spaulding *et al.*, 2010; Rost & Fritsen, 2014). Although the potential for impact on fish communities has been the greatest concern, there is scant evidence that fish communities are altered, except at local scales (Bothwell & Spaulding, 2008; Gillis, pers. comm.). Documentation of the negative impact of *D. geminata* on tadpole energetics, however, is an intriguing illustration of the importance of diatoms and their quality as food for other organisms (Furey *et al.*, 2014). Macroinvertebrate composition, total biomass, and distribution of size classes have been well-documented as strongly and predictably related to amount of stalk material (Kilroy *et al.*, 2009; Gillis & Chalifour, 2010; Rost & Fritsen, 2014). In ecological assessments, nuisance growths of *D. geminata* are correlated with invertebrate metrics similar to those impacted by pollutants, watershed disturbance, and high nutrient concentrations.

At the same time, however, streams and rivers with nuisance growths of *D. geminata* are <u>not</u> highly impacted by the often-common suite of anthropogenic pressures, such as high nutrient concentrations, fine sediment loads and organic compounds. Indeed, the ongoing, compelling paradox of *D. geminata* is its ability to form large amounts of stalk material under nutrient poor conditions (Bothwell & Kilroy, 2011; Kilroy & Bothwell, 2011; Sundareshwar *et al.*, 2011; Cullis *et al.*, 2012). This diatom thrives in the most oligotrophic of waters (Bothwell *et al.*, 2014) and, even at nuisance levels, may serve as an indication of clean waters. Most recently, attention has shifted from the primacy of proliferation and spread of *D. geminata* to suggestions of the role of environmental change (Bothwell *et al.*, 2014; Lavery *et al.*, 2014; Taylor & Bothwell, 2014). Furthermore, *D. geminata* can be transported to new habitats, but human-induced environmental alteration may also further the success of the species. Investigation of the role of environmental change and interaction with human vectors will aid in further understanding the complexities and invasiveness of this organism. More research on distribution, controlling factors and habitat window for *D. geminata* is needed (Cullis *et al.*, 2012; Hammond, 2013). Only then will we be able to effectively manage *D. geminata* mats at the regional or watershed scale.

It is not uncommon for basic information regarding nuisance species to be unknown or uncertain. Despite the lack of information, management responses are proactively implemented (Simberloff, 2003). Rout *et al.* (2014) suggest a combined strategy of determining species distributions and implementing specific management actions, rather than waiting to resolve issues of distribution before responding with action. Similarly, addressing unresolved aspects regarding *D. geminata* while concurrently taking steps to minimize spread of *D. geminata* is a proactive strategy. Minimizing the spread of *D. geminata* may be the least intrusive action and could reduce the transfer of other nuisance and invasive aquatic species.

11.1 Recommendation for managers

Communication with the public regarding *D. geminata* should be such that the outreach message covers generalized aquatic invasive species prevention. As more scientific details emerge from current and ongoing work, focusing on the preventive strategy of *check, clean, dry and/or freeze* the inadvertent transportation of living cells will be reduced, while also avoiding the transportation of other invasive species and pathogens. This is not a decontamination protocol, but rather a recommendation to propagate the current public awareness message.

Every time equipment or gear is moved between waterways, precautions need to be taken:

CHECK and remove aquatic plants, animals, and mud from equipment and gear at the site of origin

CLEAN and thoroughly wash equipment and gear

DRY equipment and gear completely, or **FREEZE**

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ANNEXE 1
GUIDE DU BÉNÉVOLE

GUIDE DE SUIVI - ALGUE DIDYMO

Dans le cadre du projet de recherche : “Suivi de la sévérité des proliférations et compréhension des facteurs contrôlant sa variabilité”

CIRSA
Centre interuniversitaire
de recherche sur
le saumon atlantique

Le Conseil de l'eau du Nord de la Gaspésie

INRS
Université d'avant-garde

MERCI AUX PARTENAIRES

Conseil de gestion du bassin-versant de la Rivière Restigouche inc
Restigouche River Watershed Management Council Inc.
CGBVRR RRWMC

The Atlantic Salmon Conservation Foundation
La fondation pour la conservation du saumon atlantique

CGRMP

Gespe'gewaq Mi'gmaq Resource Council

Natural Resource Directorate
Listuguj Fisheries

Organisme de bassin versant Matapédia-Restigouche Watershed Organization

Le Conseil de l'eau du Nord de la Gaspésie

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IMPORTANCE DU RÉSEAU DE SUIVI

Un réseau formé de bénévoles assure le suivi hebdomadaire de la prolifération de didymo sur plusieurs rivières de l'est du Québec et du Nouveau-Brunswick.

Avec l'aide des bénévoles, nous serons en mesure d'avoir des renseignements précis sur la présence-absence et la sévérité de didymo. Cette banque de données servira à discriminer les facteurs environnementaux pouvant favoriser ou limiter l'occurrence et l'ampleur des proliférations.

L'algue didymo est présente dans les rivières à saumon du Québec depuis 2006. Elle est maintenant observée sur la quasi-totalité des rivières de la Gaspésie et du nord du Nouveau-Brunswick. Jusqu'à tout récemment, l'algue didymo n'avait pas été répertoriée au nord du fleuve St-Laurent. L'algue didymo a été observée pour la première fois sur la rivière à mars au Saguenay à l'automne 2014.

Ainsi, la contribution substantielle des bénévoles dans ce projet, nous permettra de poursuivre notre acquisition de connaissances sur cette algue émergente.

Photo : Carole-Anne Gillis

L'ALGUE DIDYMO

QU'EST-CE QUE L'ALGUE DIDYMO ?

L'algue didymo est une algue unicellulaire microscopique à potentiel envahissant. Il s'agit d'une diatomée comportant un squelette externe composé de silice. Les cellules produisent une tige fibreuse avec laquelle elles peuvent s'accrocher aux roches. Lorsqu'elle prolifère, les tiges forment des tapis fibreux d'un jaune-brunâtre au blanc sur le lit des rivières. L'algue didymo a la texture de la laine mouillée, d'aspect visqueux et cotonneux. Une fois séchés, les amas d'algues ressemblent à du papier hygiénique.

PRÉFÉRENCES D'HABITATS

L'algue didymo préfère les rivières peu profondes à eau froide et claire avec un fond de gravier stable. Elle préfère également l'eau pauvre en éléments nutritifs et des eaux de pH neutre à basique. Lorsque toutes les conditions favorables à son développement sont réunies, elle peut proliférer rapidement et envahir entièrement le lit des rivières.

Photo : Andrew Olive

Photo : Didymo tapissant le lit d'une rivière

Photo : Organisme du Bassin Versant Matapedia-Restigouche

Photo : Amas de didymo séchés sur la rive

PROPAGATION OU NON?

Cette algue est native à l'Amérique du nord ainsi qu'à l'est du Canada. Cette algue microscopique est considérée rare, toutefois, depuis les années 2000, son occurrence a considérablement augmentée à travers le monde. La modification des facteurs environnementaux à l'échelle planétaire seraient la principale cause de son émergence et créant par conséquent des milieux aquatiques favorables à sa prolifération. Toutefois, nous ne pouvons nier que didymo est résistante à la dessiccation et elle peut survivre jusqu'à 2 mois dans un environnement humide, tel que les semelles de feutres.


Photo : Biosecurity NZ


Photo : Guillaume Viel

COMMENT LIMITER LA PROPAGATION ?

EXAMINER son équipement et enlever toute matière qui y adhère

NETTOYER son équipement

SÉCHER complètement l'équipement qui a été en contact avec l'eau

CONGELER l'équipement lorsque cela est possible (cette dernière méthode est la plus efficace car elle éclate les cellules).

IMPACTS POTENTIELS

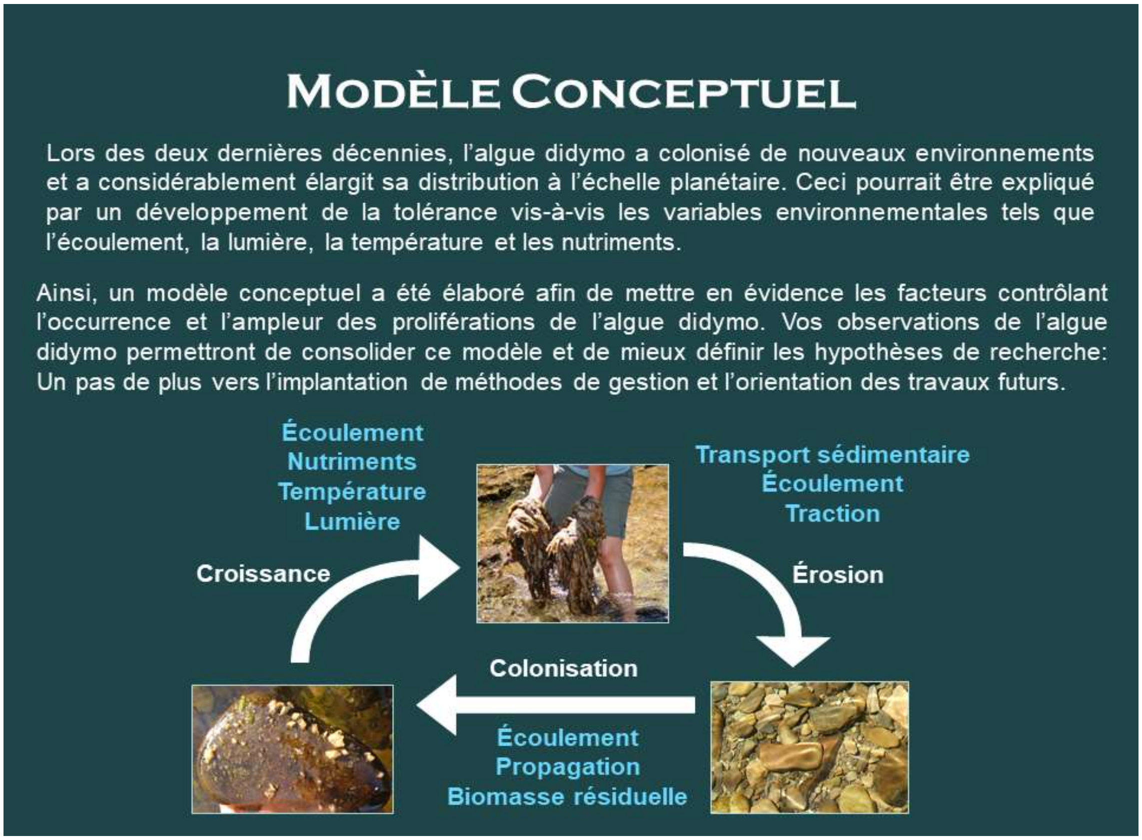
L'algue didymo n'est pas un risque à la santé humaine, mais peut diminuer la valeur esthétique des cours d'eau touchés. Les proliférations de didymo ont également un effet sur la composition des communautés de larves aquatiques et occasionne des modifications au niveau de la diète des poissons. Puisque les préférences d'habitat de l'algue didymo et du saumon atlantique juvénile se chevauchent, cette algue peut potentiellement causer des perturbations au niveau de la qualité des proies et nuisant ainsi à la croissance et la condition physique de ces salmonidés. Des travaux de recherche sont présentement en cours afin d'établir les conséquences de cette algue sur la chaine alimentaire et la qualité de l'habitat du saumon juvénile en rivière.

DISTRIBUTION ET SÉVÉRITÉ

Grâce aux données amassées dans le cadre de cet effort de suivi des proliférations de l'algue didymo, nous pouvons maintenant identifier quelques facteurs pouvant limiter la sévérité et la persistence des proliférations diverses échelles spatiales. Par exemple, à l'échelle provinciale, la distribution de l'algue didymo semble être définie par la chimie de l'eau, notamment au niveau des valeurs de pH. Les cellules de l'algue didymo ne peuvent pas survivre lorsque le pH < 7,0.

À l'échelle du bassin versant, la fréquence et l'ampleur des crues ainsi que le régime thermique qui limitent la sévérité et la durée des proliférations.

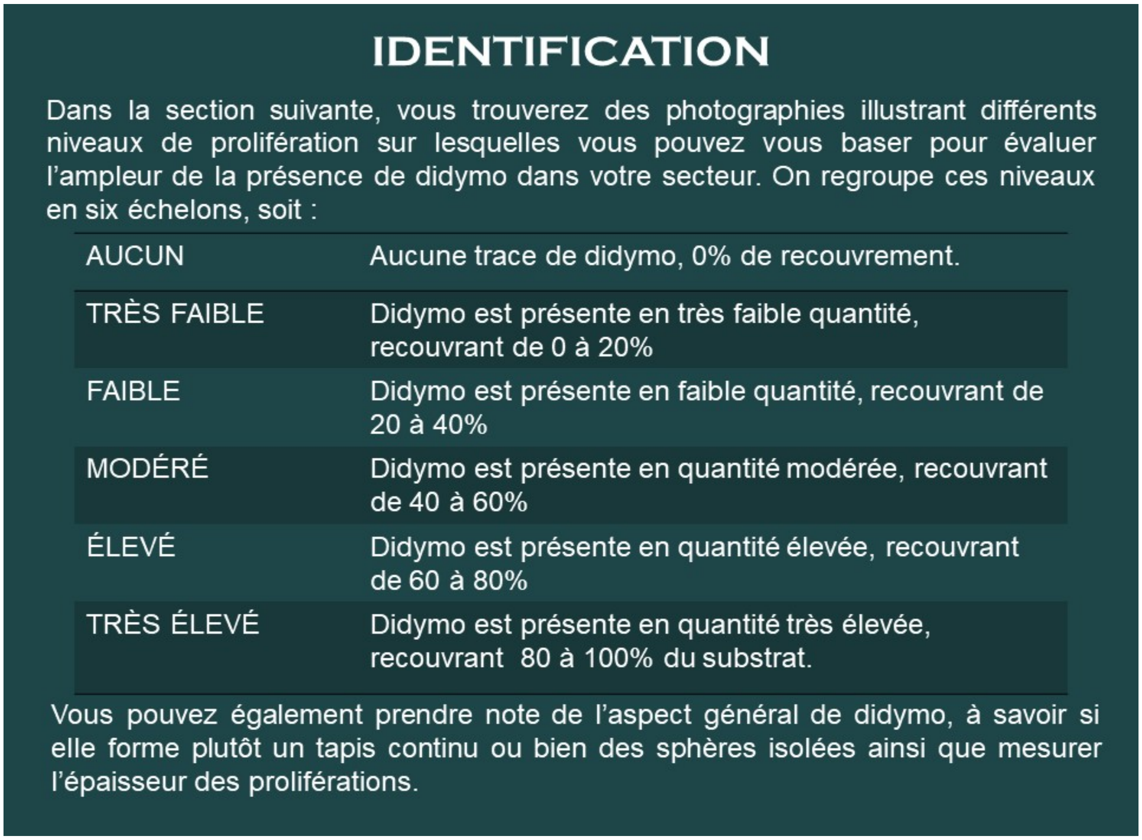
Tandis qu'à l'échelle du cours d'eau, ce sont la luminosité et le facies d'écoulement qui régissent sa présence et son ampleur.



MODÈLE CONCEPTUEL

Lors des deux dernières décennies, l'algue didymo a colonisé de nouveaux environnements et a considérablement élargit sa distribution à l'échelle planétaire. Ceci pourrait être expliqué par un développement de la tolérance vis-à-vis les variables environnementales tels que l'écoulement, la lumière, la température et les nutriments.

Ainsi, un modèle conceptuel a été élaboré afin de mettre en évidence les facteurs contrôlant l'occurrence et l'ampleur des proliférations de l'algue didymo. Vos observations de l'algue didymo permettront de consolider ce modèle et de mieux définir les hypothèses de recherche: Un pas de plus vers l'implantation de méthodes de gestion et l'orientation des travaux futurs.



IDENTIFICATION

Dans la section suivante, vous trouverez des photographies illustrant différents niveaux de prolifération sur lesquelles vous pouvez vous baser pour évaluer l'ampleur de la présence de didymo dans votre secteur. On regroupe ces niveaux en six échelons, soit :

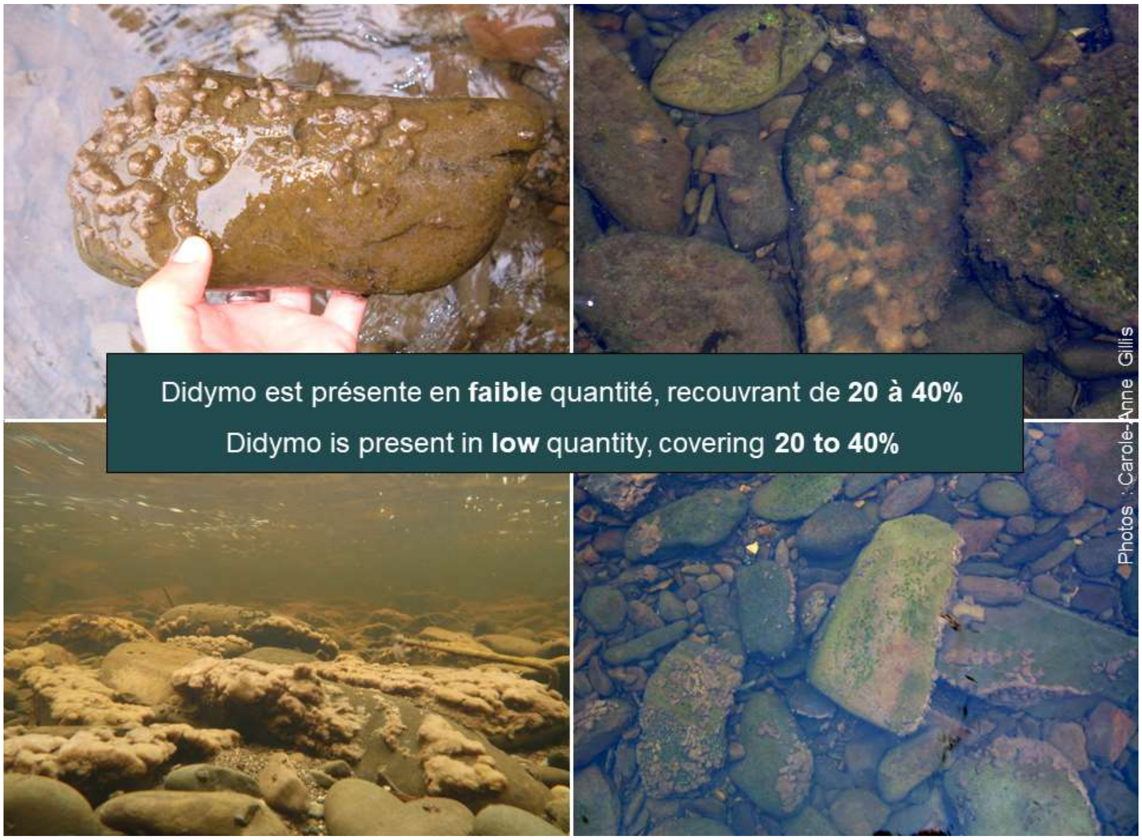
AUCUN	Aucune trace de didymo, 0% de recouvrement.
TRÈS FAIBLE	Didymo est présente en très faible quantité, recouvrant de 0 à 20%
FAIBLE	Didymo est présente en faible quantité, recouvrant de 20 à 40%
MODÉRÉ	Didymo est présente en quantité modérée, recouvrant de 40 à 60%
ÉLEVÉ	Didymo est présente en quantité élevée, recouvrant de 60 à 80%
TRÈS ÉLEVÉ	Didymo est présente en quantité très élevée, recouvrant 80 à 100% du substrat.

Vous pouvez également prendre note de l'aspect général de didymo, à savoir si elle forme plutôt un tapis continu ou bien des sphères isolées ainsi que mesurer l'épaisseur des proliférations.

Didymo est présente en **très faible** quantité, recouvrant de **0 à 20%**

Didymo is present in **very low** quantity, covering **0 to 20%**

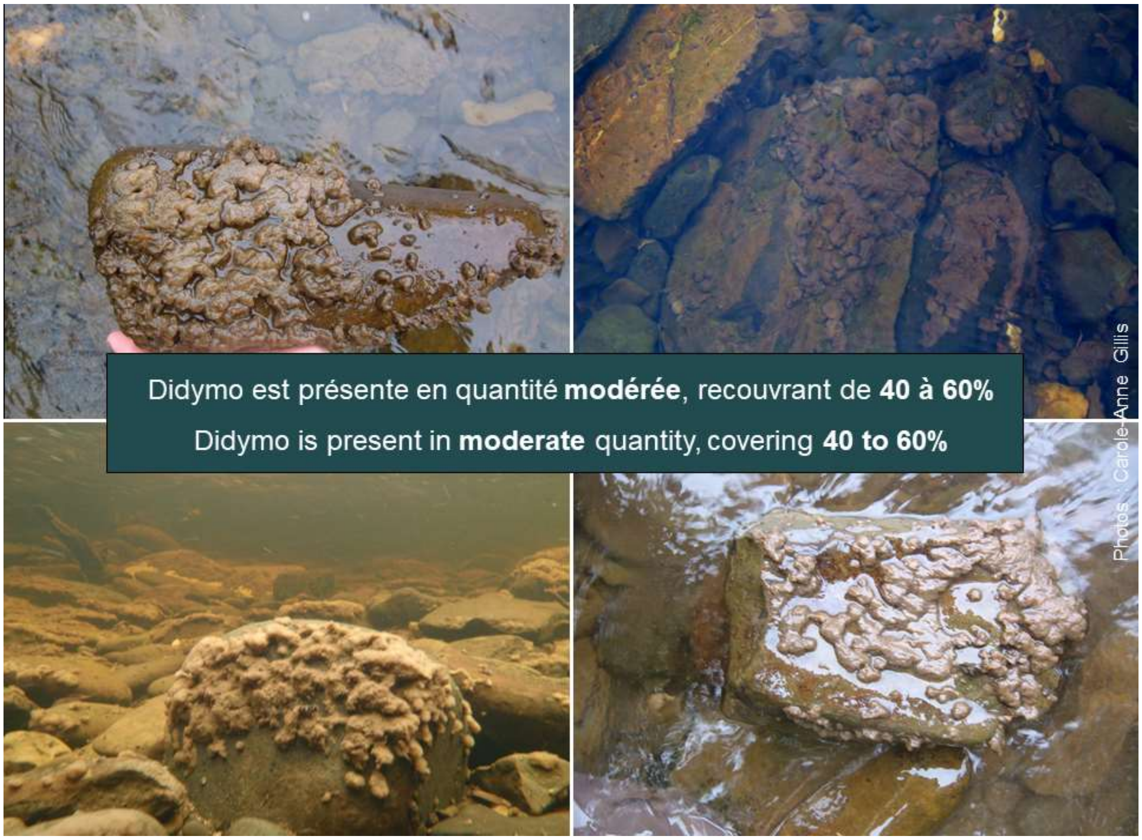
Photos : Carole-Anne Gillis



Didymo est présente en **faible** quantité, recouvrant de **20 à 40%**

Didymo is present in **low** quantity, covering **20 to 40%**

Photos : Carole-Anne Gillis



Didymo est présente en quantité **modérée**, recouvrant de **40 à 60%**

Didymo is present in **moderate** quantity, covering **40 to 60%**

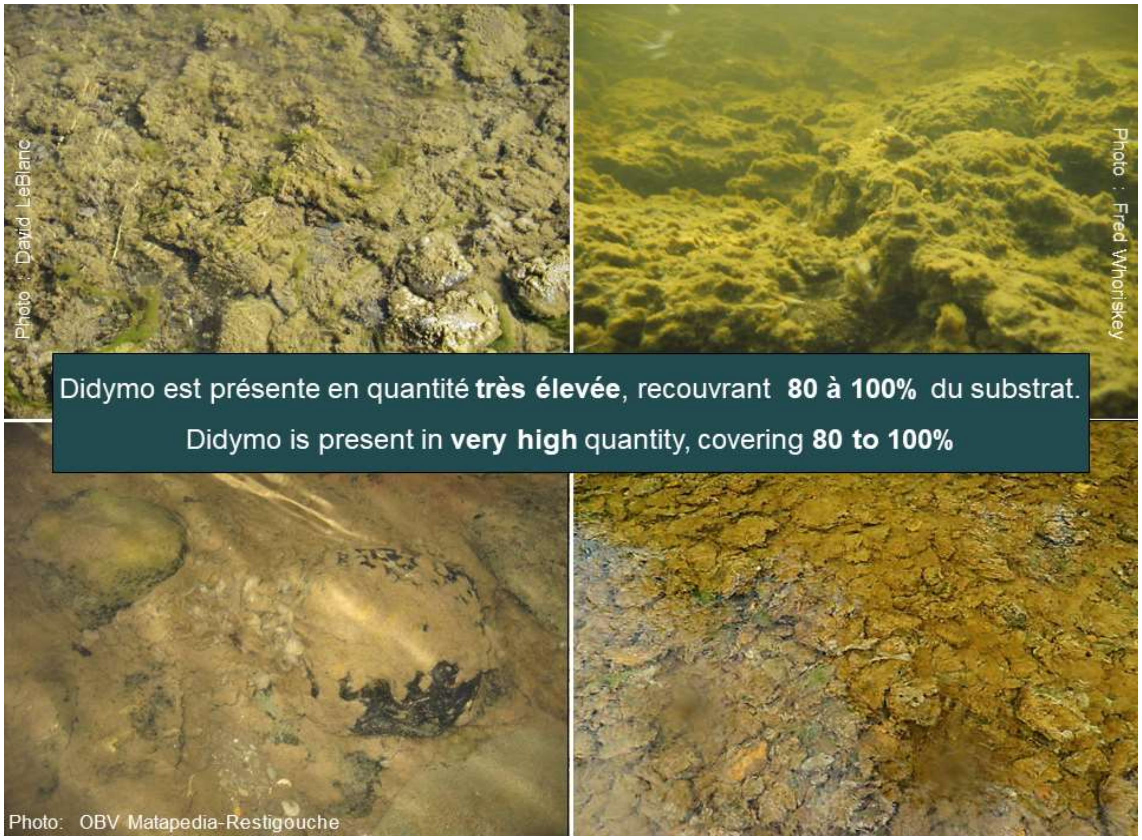
Photos : Carole-Anne Gillis

Didymo est présente en quantité **élevée**, recouvrant de **60 à 80%**
Didymo is present in **high** quantity, covering **60 to 80%**

Photo: OBV Matapedia-Restigouche

Photo: Justin Murdock

Photos : Carole-Anne Gillis



Didymo est présente en quantité **très élevée**, recouvrant **80 à 100%** du substrat.

Didymo is present in **very high** quantity, covering **80 to 100%**

Photo : David LeBlanc

Photo : Fred Whoriskey

Photo: OBV Matapedia-Restigouche

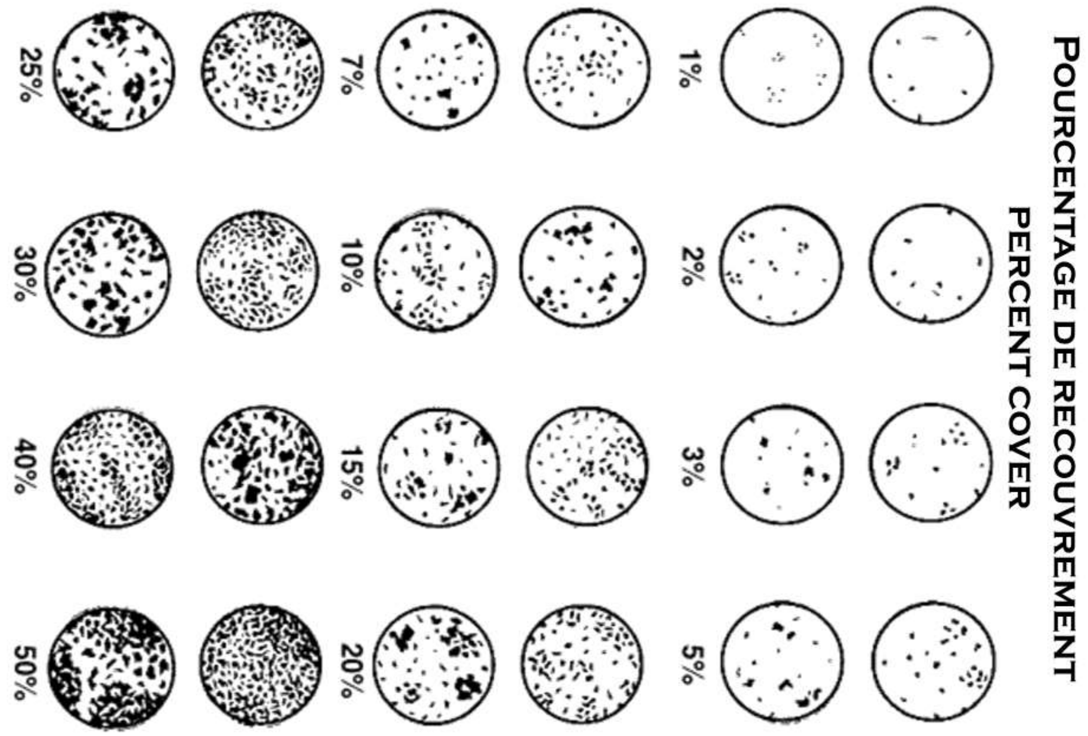
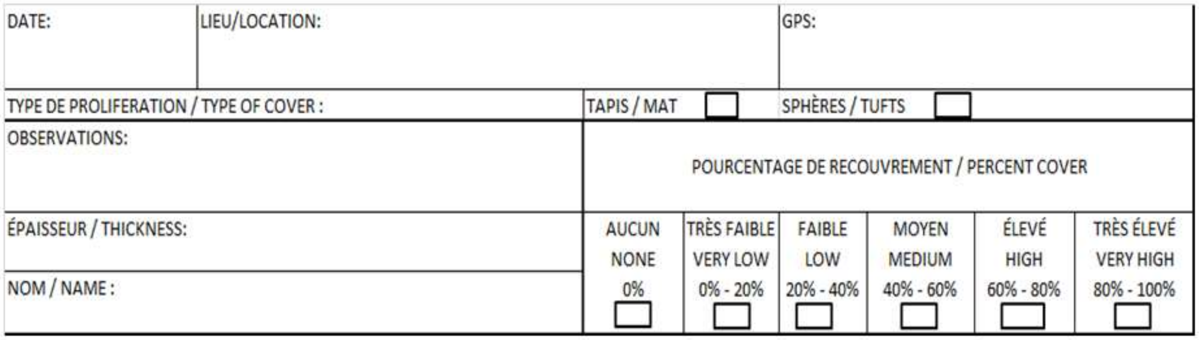
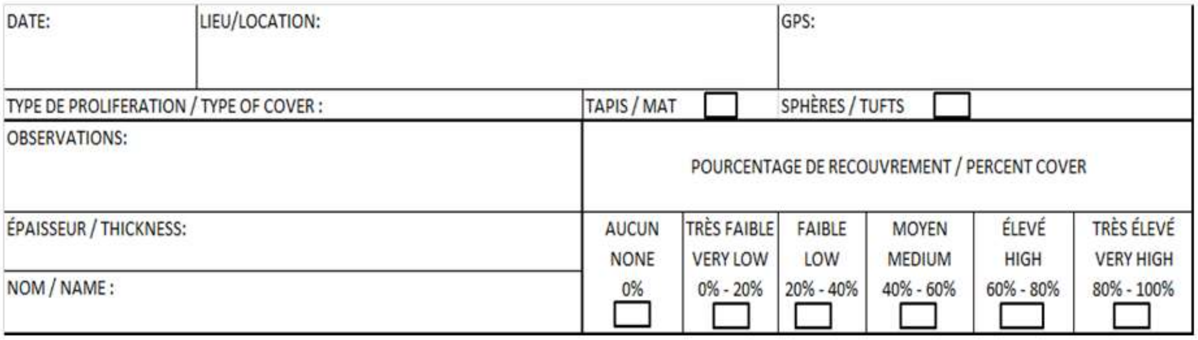


Image : www.ilmb.gov.bc.ca



DATE:	LIEU/LOCATION:		GPS:			
TYPE DE PROLIFERATION / TYPE OF COVER :	TAPIS / MAT ☐		SPHÈRES / TUFTS ☐			
OBSERVATIONS:	POURCENTAGE DE RECOUVREMENT / PERCENT COVER					
ÉPAISSEUR / THICKNESS:	AUCUN NONE 0% ☐	TRÈS FAIBLE VERY LOW 0% - 20% ☐	FAIBLE LOW 20% - 40% ☐	MOYEN MEDIUM 40% - 60% ☐	ÉLEVÉ HIGH 60% - 80% ☐	TRÈS ÉLEVÉ VERY HIGH 80% - 100% ☐
NOM / NAME :						



DATE:	LIEU/LOCATION:		GPS:			
TYPE DE PROLIFERATION / TYPE OF COVER :	TAPIS / MAT ☐		SPHÈRES / TUFTS ☐			
OBSERVATIONS:	POURCENTAGE DE RECOUVREMENT / PERCENT COVER					
ÉPAISSEUR / THICKNESS:	AUCUN NONE 0% ☐	TRÈS FAIBLE VERY LOW 0% - 20% ☐	FAIBLE LOW 20% - 40% ☐	MOYEN MEDIUM 40% - 60% ☐	ÉLEVÉ HIGH 60% - 80% ☐	TRÈS ÉLEVÉ VERY HIGH 80% - 100% ☐
NOM / NAME :						

ANNEXE 2
SUPPLEMENTARY TABLES FOR CHAPTER 8

Diatom assemblage data for the samples collected on thin versus thick mats collected at the RGBW site. Only the taxa composing more than 1% of the assemblage in at least one sample are presented.

	thin mat	thin mat	thick mat	thick mat
Achnanthidium cf. *gracillimum*	0	0.2	0	1.2
Achnanthidium minutissimum	75.5	69.6	41.2	35.7
Amphipleura pellucida	0.2	0.5	1.2	0.7
Delicata delicatula	0	0	1.2	0
Diatoma moniliformis	0.7	0.5	4.7	8.2
Didymosphenia geminata	0	0	0.7	2.2
Encyonopsis microcephala	1.2	1.4	2.9	1.4
Fragilaria capucina (form 1)	0	1.4	1.5	7.7
Fragilaria capucina var. *vaucheriae*	0	0.5	2.2	4.3
Fragilaria capucina var. *vaucheriae* (small form)	19.5	20.3	40	32.1
Navicula cryptotenella	0.7	2.9	2.5	1
Nitzschia fonticola	0.5	1.2	0	0.5

Diatom assemblage data for the samples collected on rocks with different levels (1 to 6) of *D. geminata* accumulation. Only the taxa composing more than 1% of the assemblage in at least one sample are presented.

	RGBW_1	RGBW_2	RGBW_3	RGBW_4	RGBW_5	RGBW_6
Achnanthidium cf. *deflexum*	0	0.2	1	2.3	0	0.5
Achnanthidium cf. *gracillimum*	1	0.7	1.2	0	0.5	2.7
Achnanthidium minutissimum	34.1	25.7	19.6	50.3	27	83.3
Brachysira microcephala	0.2	0	0	1.3	0	0.2
Cocconeis placentula	0	0.2	0	0.5	0	0
Cymbella cf. *excisiformis*	0	0	0	0.3	0.2	0.2
Delicata delicatula	2.4	0	0.2	1.8	0	0
Denticula tenuis	0	0	0	0	0	0
Diatoma ehrenbergii	0	0	0	0	0	0
Diatoma mesodon	0	0	0	0	0	0
Diatoma moniliformis	33.4	43.3	61.6	18.8	58.3	8.8
Didymosphenia geminata	1.4	1.2	3	0.5	0.2	0
Encyonema minutum	0.5	0	0	0	0	0
Encyonema silesiacum	2.4	1.9	0.5	0.5	0.5	0.5
Encyonopsis microcephala	0	0	0.7	2.3	0	0.5
Eucocconeis laevis	0.2	0.2	0	0.3	0	0.2
Fragilaria capucina (form 1)	2.9	4.6	0.5	1.5	3.2	0
Fragilaria capucina (form 2)	0.5	1	0.2	0.3	1	0
Fragilaria capucina var. *vaucheriae*	6	1.5	2.5	4.3	3.2	0
Fragilaria capucina var. *vaucheriae* (small form)	4.8	13.8	6.9	10.3	2	1.2
Gomphonema spp.	0.5	0	0.5	0.8	0.5	0
Gomphonema micropus (complex)	0	0.5	0	0.3	0.5	0
Gomphonema parvulum	0	0	0	0	0	0
Hannaea arcus	0	0.7	0	0.8	0.5	0
Navicula cryptotenella	1.7	1.2	0.5	1.8	0.5	0
Navicula cryptotenelloides	1.2	0	0.2	0.8	0	0
Navicula reichardtiana	0	0	0	0	0	0
Nitzschia agnita	0	0	0	0	0	0
Nitzschia dissipata	1.4	0.2	0	0.3	1	0
Nitzschia pura	0	0	0	0	0	0
Pseudostaurosira brevistriatta	0	0	0	0	0	0
Staurosira construens	0	0	0	0	0	0
Staurosira construens var. *venter*	0	0	0	0	0	0
Staurosirella pinnata	0	0	0	0	0	0

	RGBP_1	RGBP_2	RGBP_3	RGBP_4	RGBP_5	RGBP_6
Achnanthidium cf. *deflexum*	4.6	4.7	5.1	21.2	35.2	30.3
Achnanthidium cf. *gracillimum*	1	0.5	1.4	4.9	6.2	1.2
Achnanthidium minutissimum	30	40.9	61.6	40.1	39	43.3
Brachysira microcephala	0	0	0.5	0	0	0
Cocconeis placentula	0.7	0.7	0.5	0.7	0.2	0
Cymbella cf. *excisiformis*	0.5	0.2	0.5	1.2	0	0
Delicata delicatula	0	0.7	0	0.5	0	0
Denticula tenuis	0.5	0	0	0	0	0
Diatoma ehrenbergii	3.4	4.9	2.9	2.2	1.7	0.2
Diatoma mesodon	0	0	0	0	0	0
Diatoma moniliformis	15.9	11.5	6.8	3.4	2.4	9.2
Didymosphenia geminata	1.4	0	0.7	2.2	0.5	0.2
Encyonema minutum	0	0	0	0	0	0
Encyonema silesiacum	11.8	5.6	3.9	4.9	1	2.7
Encyonopsis microcephala	0.5	0.9	0	4.9	2.6	1.2
Eucocconeis laevis	0.5	0	0	0	0	0.2
Fragilaria capucina (form 1)	1	0.7	1.7	0.5	1	0.5
Fragilaria capucina (form 2)	2.4	5.9	1.2	3.2	2.6	1
Fragilaria capucina var. *vaucheriae*	4.8	0.7	2.2	0.5	0.2	0
Fragilaria capucina var. *vaucheriae* (small form)	2.7	4.9	2.4	0.5	0	2.7
Gomphonema spp.	0.7	0.5	0.2	0	0	0
Gomphonema micropus (complex)	0	0	0	0	1.2	0.5
Gomphonema parvulum	0	0	0	0	0	1
Hannaea arcus	7.7	8.5	5.8	4.1	3.6	2.7
Navicula cryptotenella	0.5	0	0	0	0	0
Navicula cryptotenelloides	0.5	0.7	0	0	0	0
Navicula reichardtiana	1.7	0.5	0	0.7	0	0.5
Nitzschia agnita	1.4	0	0	0	0	0
Nitzschia dissipata	0	0.2	0	0	0	0
Nitzschia pura	1.4	0	0	1	0	0
Pseudostaurosira brevistriatta	0	0	0	0	0	0
Staurosira construens	0	0	0	0	0	0
Staurosira construens var. *venter*	0	0	0	0	0	0
Staurosirella pinnata	0	0	0	0	0	0

	RRMH_1	RRMH_2	RRMH_3	RRMH_4	RRMH_5	RRMH_6
Achnanthidium cf. *deflexum*	2.1	4.7	1	5.6	5.1	5.4
Achnanthidium cf. *gracillimum*	10.7	8.3	13.8	9.6	15.6	7
Achnanthidium minutissimum	43.2	45.2	40.1	43	37.7	46.9
Brachysira microcephala	1	0	0	0.7	1	0.5
Cocconeis placentula	0	0	0	0	0.2	0
Cymbella cf. *excisiformis*	0	0	0.5	1.2	1	0.9
Delicata delicatula	1.7	0.5	2	0.7	2	1.4
Denticula tenuis	0	0	0.2	0	0	0.2
Diatoma ehrenbergii	3.8	0	2.2	1.4	0.7	1.2
Diatoma mesodon	0	0	0	0	0	0
Diatoma moniliformis	9.3	10.1	6.7	12.7	8.3	11.3
Didymosphenia geminata	0	0.5	1	0.9	0.7	1.6
Encyonema minutum	0.2	1.6	1.2	0	1.5	0.9
Encyonema silesiacum	4.1	6.2	7.6	4.5	9.5	3.8
Encyonopsis microcephala	0.5	1	1.2	1.9	1	1.6
Eucocconeis laevis	0	1	0	0	0	0
Fragilaria capucina (form 1)	2.4	3.9	2.2	1.9	1	1.6
Fragilaria capucina (form 2)	3.3	0	0	1.2	0.7	0.9
Fragilaria capucina var. *vaucheriae*	2.1	3.4	0	1.2	2.4	1.6
Fragilaria capucina var. *vaucheriae* (small form)	6	6.8	12.6	7.3	5.4	6.3
Gomphonema spp.	0	0.5	1.7	1.2	1.2	0.9
Gomphonema micropus (complex)	0.2	0	0	0	0	0
Gomphonema parvulum	0	0	0	0	0	0
Hannaea arcus	2.4	2.3	2	1.4	2	2.3
Navicula cryptotenella	1	0.5	0.7	0.2	0.5	0
Navicula cryptotenelloides	0	0	0	0	0	0
Navicula reichardtiana	0	0.8	0	0	0	0
Nitzschia agnita	0.5	0	0	0	0.5	0
Nitzschia dissipata	0.5	0	0	0	0	0.2
Nitzschia pura	0	0	0	0.5	0	0
Pseudostaurosira brevistriatta	0	0	0	0	0	0
Staurosira construens	0	0	0	0	0	0
Staurosira construens var. *venter*	1	0	0	0	0	0
Staurosirella pinnata	0	0.3	0	0.2	0	0

	PAT2M_1	PAT2M_2	PAT2M_3	PAT2M_4	PAT2M_5	PAT2M_6
Achnanthidium cf. *deflexum*	14.6	13.5	15.8	16.2	28.8	36
Achnanthidium cf. *gracillimum*	33.8	24.3	12.2	8	12	4.4
Achnanthidium minutissimum	23.1	25.2	24	21.6	24.7	36.3
Brachysira microcephala	0	0	0	0	0	0
Cocconeis placentula	0	0.2	0.5	0.2	0.2	0.9
Cymbella cf. *excisiformis*	0.5	0	0.7	0	0	0
Delicata delicatula	0	0.2	0	0	0	0
Denticula tenuis	0.2	0	0	0	0	0
Diatoma ehrenbergii	1.9	3.4	4.8	3.5	5	2.7
Diatoma mesodon	0	0	0.5	0.5	0.5	0
Diatoma moniliformis	1	0	1.7	0.7	1	0.6
Didymosphenia geminata	0.7	1.2	2.6	2.8	0.2	0.6
Encyonema minutum	1.5	1	3.1	0.7	1.7	1.8
Encyonema silesiacum	11.2	16.8	23.5	28.9	12.5	5.3
Encyonopsis microcephala	0	1	0	0.5	0.5	0
Eucocconeis laevis	0.5	0.2	0.2	0.9	0.5	0
Fragilaria capucina (form 1)	1.5	1.2	1.4	1.9	2.4	1.5
Fragilaria capucina (form 2)	0.2	1.4	0	0	0.5	0
Fragilaria capucina var. *vaucheriae*	1	0.2	1.2	0.2	1.4	1.2
Fragilaria capucina var. *vaucheriae* (small form)	3.6	2.6	1.7	4.7	3.1	1.5
Gomphonema spp.	0	1.2	1	0	1.4	1.5
Gomphonema micropus (complex)	0	0	0	0	0	0.3
Gomphonema parvulum	0	0	0	0	0	0.3
Hannaea arcus	0.7	1.7	1	2.6	1.9	0.9
Navicula cryptotenella	0.2	0	0	0	0	0
Navicula cryptotenelloides	0	0.5	0	0	0	0
Navicula reichardtiana	0	0	0.5	0	0	0
Nitzschia agnita	0	0	0	0	0	0
Nitzschia dissipata	0	0	0	0.2	0	0
Nitzschia pura	0	0.5	0	0	0	0
Pseudostaurosira brevistriatta	0	0	0	0	0	1.8
Staurosira construens	0	0	0	0	0	0
Staurosira construens var. *venter*	1.2	0	0	0	0	0
Staurosirella pinnata	0	1.4	0.7	0	0	0

	PAT7M_1	PAT7M_2	PAT7M_3	PAT7M_4	PAT7M_5	PAT7M_6
Achnanthidium cf. *deflexum*	23	24.1	13	20.5	16.7	42.8
Achnanthidium cf. *gracillimum*	9.1	20.2	8	10.8	25.6	16.2
Achnanthidium minutissimum	22.7	16.3	17.9	12.5	8.6	18.4
Brachysira microcephala	0	0	0	0	0	0
Cocconeis placentula	0.2	0.7	0.7	0.5	0.2	2.9
Cymbella cf. *excisiformis*	0.5	0	0	0	0	0
Delicata delicatula	0	0	0.2	0	0	0
Denticula tenuis	0	0	0	0	0	0
Diatoma ehrenbergii	3.7	1.9	3.9	7.2	6.4	0.7
Diatoma mesodon	0.2	0	0.2	0.7	1.7	0
Diatoma moniliformis	1.2	0.2	0	1.4	0.5	0.7
Didymosphenia geminata	1.6	1.2	2.2	4.1	3.9	0.7
Encyonema minutum	1.9	4.6	4.6	1.2	2.2	0.2
Encyonema silesiacum	19.9	15.8	35.7	28.9	17	6
Encyonopsis microcephala	0.7	0.5	0	0	0	0
Eucocconeis laevis	0.7	0.2	0.2	0	0	0
Fragilaria capucina (form 1)	0.9	1	1	2.4	1.5	1.2
Fragilaria capucina (form 2)	0.7	1	0	1.4	0	0.2
Fragilaria capucina var. *vaucheriae*	0.7	1.9	0.5	2.2	2	0
Fragilaria capucina var. *vaucheriae* (small form)	3	1.7	1.7	2.4	3.7	1.4
Gomphonema spp.	0.5	0.2	0.7	0.5	0	0
Gomphonema micropus (complex)	0.7	0.5	0.7	0	0	0.5
Gomphonema parvulum	0	0	0	0	0	2.9
Hannaea arcus	2.8	3.2	1.4	1.2	4.7	1
Navicula cryptotenella	0.2	0	0	0	0	0.2
Navicula cryptotenelloides	0	0	0	0	0	0
Navicula reichardtiana	0	0	0.2	0	0	0.2
Nitzschia agnita	0	0	0	0	0	0
Nitzschia dissipata	0	0	0.2	0	1.5	0
Nitzschia pura	0	0	0.2	0	0	0
Pseudostaurosira brevistriatta	0	0	0	0	0	0
Staurosira construens	0	0	1.7	0	0.2	0
Staurosira construens var. *venter*	0.2	0	0.7	0	1.7	0
Staurosirella pinnata	0.2	0.2	0.5	0	0	0.5

	RRBB_1	RRBB_2	RRBB_3	RRBB_4	RRBB_5	RRBB_6
Achnanthidium cf. *deflexum*	4.4	9.4	12.8	11.4	8.9	13.8
Achnanthidium cf. *gracillimum*	43.4	28.7	27.6	31.9	15.4	10.8
Achnanthidium minutissimum	23.8	31.9	26.9	35	53.7	52
Brachysira microcephala	0.2	0	0.5	0	0	0
Cocconeis placentula	0	0	0	0	0	0
Cymbella cf. *excisiformis*	2.4	0	0.7	1.4	0.5	2.2
Delicata delicatula	1.7	0	1	0.2	0	1
Denticula tenuis	1.2	1	0.7	0.2	0.2	0.2
Diatoma ehrenbergii	0	0	0.2	0.5	1.2	0.2
Diatoma mesodon	0	0	0	0.2	0	0
Diatoma moniliformis	1.2	0.5	0.5	2.7	1	1
Didymosphenia geminata	0	0	0.5	0.7	0	1
Encyonema minutum	2.4	1.2	4.1	0.5	2.7	1
Encyonema silesiacum	10.4	14.5	12.6	5.3	9.4	9.9
Encyonopsis microcephala	1.7	1.7	2.4	1.7	1	0.5
Eucocconeis laevis	0.5	0.2	0	1.4	1	0
Fragilaria capucina (form 1)	0	0.7	0.2	0.2	0.5	1.7
Fragilaria capucina (form 2)	0.2	1.4	0	1.2	0	0.7
Fragilaria capucina var. *vaucheriae*	0	0	0.2	0	0.5	0
Fragilaria capucina var. *vaucheriae* (small form)	1.2	1.4	1.2	0.5	0.2	1
Gomphonema spp.	1.9	2.9	0.5	1.4	1.7	0.5
Gomphonema micropus (complex)	0	0	0	0	0	0
Gomphonema parvulum	0	0	0	0	0	0
Hannaea arcus	0	0.5	0	0	0	0
Navicula cryptotenella	1.7	0.5	0.7	0.5	0	0.7
Navicula cryptotenelloides	0	0	0	0	0	0
Navicula reichardtiana	0	0.5	1	0.2	0	0
Nitzschia agnita	0	0	0.7	0	0	0
Nitzschia dissipata	0	0	0	0.2	0	0
Nitzschia pura	0	0	0	0	0.5	0
Pseudostaurosira brevistriatta	0	0	0	0	0	0
Staurosira construens	0	0	0	0	0	0
Staurosira construens var. *venter*	0	0	1	0	0	0
Staurosirella pinnata	0.5	1	0	0	0	0