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PATRONS DE DISTRIBUTION ET DE DIVERSITÉ DU PHYTOPLANCTON LACUSTRE

THÉSE
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PAR
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AVANT-PROPOS

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TABLE DES MATIÈRES

LISTE DES FIGURES

LISTE DES TABLEAUX

RÉSUMÉ

L'hétérogénéité spatiale dans la colonne d'eau d'un lac joue un rôle important sur le contrôle de la distribution du phytoplancton et sur le maintien de sa diversité. Des gradients verticaux environnementaux (p. ex. de température, de lumière ou de nutriments) bien prononcés favorisent la distribution du phytoplancton dans des couches plus définies et, à travers une différenciation des niches disponibles pour plus d'espèces, sa diversité. Ces relations entre l'hétérogénéité de l'habitat et le phytoplancton ont été montrées par des études expérimentales ou à partir d'observations sur un ou quelques lacs. Cependant, il reste à déterminer si les patrons pour un ensemble de lacs présentant différentes caractéristiques morphométriques et chimiques sont conformes à ces attentes et si la diversité fonctionnelle se révélera plus sensible à ces gradients que les indices taxonomiques traditionnels.

Dans les lacs tempérés de l'Hémisphère Nord, la thermocline estivale et le gradient de lumière dans la colonne d'eau constituent les principales structures physiques susceptibles d'affecter le phytoplancton. L'objectif principal de cette étude était ainsi d'évaluer comment la structure physique de la colonne d'eau [pénétration de lumière, profondeur et forme (coefficient de variation de la température) de la thermocline et résistance thermique relative au mélange] affecte la distribution et la diversité du phytoplancton. Les mesures de distribution utilisées incluent la profondeur du maximum de biomasse et le coefficient de variation de la chlorophylle *a* totale et des différents groupes spectraux de phytoplancton, tandis que pour la diversité deux indices taxonomiques (la richesse en espèces et l'indice de Shannon) et un indice de diversité fonctionnelle ont été utilisés. Afin d'atteindre cet objectif, 45 lacs de deux régions distinctes du Sud du Québec (Canada), l'Estrie et les Laurentides, ont été examinés. Les deux régions diffèrent dans la géologie de leurs bassins versants et dans leur chimie de l'eau. Les patrons dans la distribution, la composition et la diversité du phytoplancton au regard des facteurs environnementaux ont également été examinés dans 18 lacs de l'Estrie lors de trois périodes distinctes de la stratification estivale : le printemps tardif, la mi-été et le début de l'automne.

Les résultats de cette étude ont montré que pour l'ensemble des lacs, des gradients plus prononcés de température favorisaient la distribution du phytoplancton dans des couches plus définies de biomasse, tandis que le maximum de chlorophylle *a* était plus profond dans les lacs présentant des eaux plus claires et caractérisés par un coefficient de variation de la température plus élevé. D'autre part, la distribution des différents groupes de phytoplancton était distinctement reliée à la couleur de l'eau et à la concentration du phosphore total dans l'épilimnion. En comparant les deux régions, les lacs des Laurentides ont montré des thermoclines moins profondes, et un coefficient de variation de la température ainsi qu'une résistance thermique relative au mélange plus élevés que dans les lacs de l'Estrie. Par conséquent, la biomasse totale et la biomasse des groupes spectraux de phytoplancton étaient distribuées de façon plus hétérogène dans les Laurentides.

Sur l'ensemble des lacs, les indices de diversité s'appuyant sur la taxonomie traditionnelle étaient plus élevés dans les lacs présentant une plus grande hétérogénéité verticale de la température mais sujets au mélange induit par le vent. L'indice de Shannon était également plus faible dans les lacs plus eutrophes. L'autre indice de diversité, la

diversité fonctionnelle, était uniquement et plus fortement relié à la profondeur maximale du lac, une variable qui intègre d'autres variables physiques associées à la différentiation et à la stabilité de l'habitat pour le phytoplancton (p. ex. le coefficient de variation de la température et la résistance thermique relative au mélange). Alors que les mesures de diversité taxonomique différaient peu entre les régions, la diversité fonctionnelle était plus élevée en Estrie. D'autre part, l'indice de Shannon et la diversité fonctionnelle diminuaient avec la profondeur maximale du lac en Estrie, mais suivant une relation opposée dans les Laurentides.

Dans la plupart des lacs étudiés, les changements dans la composition des communautés phytoplanctoniques durant la saison de croissance suivaient le patron de succession du phytoplancton prédit pour les lacs dimictiques tempérés, sauf pour quelques exceptions. Dans les trois périodes examinées, des gradients de température plus prononcés favorisaient la distribution du phytoplancton dans des couches plus définies, alors que le maximum de biomasse était moins profond dans les lacs eutrophes avec peu ou pas de stratification. La position verticale du maximum de biomasse des différents groupes de phytoplancton ne variait pas avec la période examinée, alors que leur biomasse était distribuée de façon plus homogène au début de l'automne, particulièrement pour les cyanophytes et les cryptophytes. Cependant, la plus grande variation temporelle dans les variables phytoplanctoniques a été observée pour les trois mesures de diversité, avec des valeurs plus élevées à la mi-été quand la stratification thermique était plus prononcée et plus stable.

En conclusion, les résultats de cette étude montrent que pour un ensemble de lacs une hétérogénéité spatiale plus élevée de la colonne d'eau favorise la formation d'agrégats de phytoplancton et sa diversité. De plus, l'indice de diversite fonctionelle montre des réponses plus simples et plus fortes aux facteurs environnementaux que les indices de diversité taxonomique traditionnels.

Mots clés : phytoplancton, distribution verticale, diversité, hétérogénéité de l'habitat, structure thermique, lumière

INTRODUCTION

Le phytoplancton joue un rôle clé dans l'écologie des écosystèmes aquatiques. En effet, étant à la base de la chaîne trophique, un changement dans sa biomasse, sa distribution et/ou sa composition peut affecter les niveaux trophiques supérieurs (Brett *et al.*, 2009; Danielsdottir, Brett et Arhonditsis, 2007; Gliwicz et Lampert, 1990). Les facteurs qui contrôlent la dynamique du phytoplancton dans les lacs sont nombreux, incluant entre autres les ressources limitantes pour leur croissance, le zooplancton et les perturbations environnementales (Elser et Goldman, 1991; Grover et Chrzanowski, 2004; Reynolds, 1993, 1998). Parmi ces facteurs, l'hétérogénéité spatiale de l'environnement joue un rôle important sur le contrôle de la distribution du phytoplancton et sur le maintien de sa diversité (Clegg, Maberly et Jones, 2007; Klausmeier et Litchman, 2001, Mehner, Hölker et Kasprzak, 2005; Reynolds, 1984).

L'hétérogénéité de la colonne d'eau d'un lac peut se traduire par des gradients verticaux de température ou des ressources nécessaires à la croissance du phytoplancton comme la lumière ou les nutriments (Klausmeier et Litchman, 2001; Reynolds, 1984). Ainsi, des gradients verticaux environnementaux bien prononcés favorisent la distribution du phytoplancton dans des couches minces et définies qui concentrent une grande partie de la biomasse algale (Clegg, Maberly et Jones, 2007; Klausmeier et Litchman, 2001). Des exemples d'agrégation verticale du phytoplancton sont les floraisons de surface, la formation du maximum profond de chlorophylle (en anglais DCM, pour « deep chlorophyll maximum ») ou les couches benthiques (Klausmeier et Litchman, 2001; Knapp *et al.*, 2003; Reynolds, 1984). L'hétérogénéité dans l'environnement à travers une différenciation des niches disponibles pour l'existence d'un plus grand nombre d'espèces (Clegg, Maberly et Jones, 2007; Reynolds, 1984) favorise également une augmentation de la diversité du phytoplancton (Jäger, Diehl et Schmidt, 2008; Stomp *et al.*, 2007).

Structure verticale dans les lacs : la thermocline estivale

La thermocline estivale dans les lacs tempérés de l'Hémisphère Nord constitue une des principales structures physiques de la colonne d'eau susceptibles d'affecter le phytoplancton, car elle influence la perte d'algues par sédimentation de la zone euphotique et restreint la

disponibilité en nutriments et en gaz (Fee, 1976; Reynolds, 1984). La thermocline est un gradient de température qui sépare la couche d'eau de surface plus chaude et moins dense nommée épilimnion de la couche d'eau plus sombre, plus froide et plus dense, que l'on appelle hypolimnion (Wetzel, 2001).

Les caractéristiques morphométriques d'un lac sont importantes pour la forme et la profondeur de la thermocline. En effet, la superficie, la profondeur moyenne, le volume, l'exposition au vent et le fetch (la distance maximale sur laquelle le vent peut agir à la surface du lac sans être interrompu par la terre) peuvent affecter l'efficacité du vent à mélanger la colonne d'eau et, ainsi, le transfert de chaleur vers les couches plus profondes (Fee *et al.*, 1996; Gorham et Boyce, 1989, Patalas, 1984). Généralement, les thermoclines sont plus profondes dans les lacs présentant une grande superficie ou un fetch important (Fee *et al.*, 1996; Patalas, 1984). La forme de la thermocline peut également être une fonction de la bathymétrie du lac, qui affecte les patrons de circulation et l'intensité du mélange turbulent (MacIntyre *et al.*, 1999).

En plus de la morphométrie du lac, la structure thermique estivale de la colonne d'eau est dépendante d'autres facteurs tels que les épisodes de mélange du printemps et de l'automne (propres aux lacs des zones tempérées), les événements climatiques comme les tempêtes, et la clarté de l'eau (Lampert et Sommer, 1997). En altérant la pénétration de la lumière, principale source de chaleur de la colonne d'eau, la clarté de l'eau affecte principalement la profondeur de la thermocline (Fee *et al.*, 1996; Houser, 2006; Snucins et Gunn, 2000). Ainsi, lors des floraisons algales, caractéristiques des lacs eutrophes, ou en présence de concentrations élevées en carbone organique dissous (COD) coloré, comme dans les lacs dystrophes, la pénétration de la lumière est particulièrement réduite tout comme l'épaisseur de la couche de mélange (ou épilimnion) (Fee *et al.*, 1996; Mazumder *et al.*, 1990; Snucins et Gunn, 2000). Certaines études ont cependant montré que l'effet de la lumière (transparence de l'eau) prédit mieux la profondeur de la thermocline dans les petits lacs (Fee *et al.*, 1996; Mazumder et Taylor, 1994).

Structure verticale dans les lacs : la lumière

Le profil de lumière dans la colonne d'eau constitue aussi une structure physique importante pour la distribution du phytoplancton. L'éclairement disponible pour la photosynthèse des algues est atténué dans la colonne d'eau selon une relation exponentielle du fait de l'absorption par les molécules d'eau, la matière organique dissoute et particulaire et/ou de la réflexion par la matière particulaire (Kirk, 1994). L'atténuation de la lumière dans le spectre visible (400-700 nm) dans la colonne d'eau varie selon sa qualité spectrale, les longueurs d'onde correspondant au rouge (650-700 nm) étant atténuées plus en surface, suivies par les ondes vertes (500-560 nm) puis bleues (450-500 nm). Les différents groupes de phytoplancton présentent des pigments qui leur permettent d'absorber la lumière dans différentes parties du spectre d'éclairement (Falkowski et Raven, 1997). Les différents groupes du phytoplancton pourraient ainsi maximiser l'absorption de la lumière *via* leur localisation à une profondeur donnée dans la colonne d'eau, un comportement qui, à l'échelle de la communauté, peut potentiellement permettre la coexistence d'un plus grand nombre d'espèces et contribuer à la diversité du phytoplancton (Falkowski et Raven, 1997; Stomp *et al.*, 2004, 2007).

Structure verticale dans les lacs : les nutriments

Une conséquence de la formation de la thermocline est l'établissement d'une barrière physique séparant deux couches d'eau de densité différente qui limite l'apport de nutriments de la couche profonde plus riche vers la couche de surface plus pauvre (Fee, 1979; Reynolds, 1984). De ce fait, un gradient vertical de nutriments coïncide généralement avec la présence d'une thermocline. Dans les milieux lacustres, c'est le phosphore, connu pour son rôle dans l'eutrophisation d'origine anthropique (Schlindler, 1977), qui est considéré comme l'élément nutritif limitant pour la croissance du phytoplancton. Toutefois, la théorie ressource-ratio suggère que la déviation du ratio stœchiométrique azote:phosphore de l'environnement de celui du phytoplancton (16:1) sera le facteur qui déterminera lequel de ces deux nutriments sera limitant et quelles espèces domineront la communauté phytoplanctonique d'un lac (Rhee, 1978; Rhee et Gotham, 1980).

La structure de la colonne d'eau et la distribution du phytoplancton

Les différents groupes de phytoplancton peuvent montrer des distributions verticales différentielles en réponse aux gradients de ressources essentielles (p. ex. la lumière et les nutriments) présents pendant la période de stratification estivale car ils optimisent leurs conditions de croissance en fonction de leur physiologie et de leur motilité spécifique (Clegg, Maberly et Jones, 2007; Klausmeier et Litchman, 2001; Ptacnik, Diehl et Berger, 2003). Les taxons du phytoplancton qui présentent le plus souvent une distribution verticale hétérogène sont ceux capables de modifier leur position dans la colonne d'eau soit par un mouvement actif, comme chez les flagellés, soit en régulant leur flottabilité, comme chez les cyanophytes (Clegg, Maberly et Jones, 2007; Lindholm, 1992; Visser et *al.*, 1996). Les pics de biomasse de différents groupes de phytoplancton peuvent ainsi se trouver à des profondeurs différentes : certains cyanophytes dans des floraisons de surface (Reynolds, 1984; Visser et *al.*, 1996), les cryptophytes dans le métalimnion où leur tolérance à de faibles intensités de lumière et leurs besoins élevés en concentrations de nutriments sont généralement satisfaits (Klaveness, 1988; Ptacnik, Diehl et Berger, 2003), et les diatomées, dont plusieurs espèces présentent la capacité de réduire leur vitesse de sédimentation (Davey et Heaney, 1989), dans les DCMs.

L'hétérogénéité de l'habitat et la diversité du phytoplancton

Les gradients verticaux des différents facteurs environnementaux comme la température, la lumière et les nutriments conduisent au développement d'un spectre vertical de 'microhabitats' ou niches, chacun offrant des conditions uniques qui favorisent la croissance de groupes particuliers d'espèces de phytoplancton (Clegg, Maberly et Jones, 2007; Reynolds, 1992). La présence simultanée de ces niches dans la colonne d'eau permet potentiellement le maintien d'une plus grande diversité (Jäger, Diehl et Schmidt, 2008; Stomp *et al.*, 2007). Cependant, en plus de l'hétérogénéité spatiale, il est également nécessaire, afin de permettre la coexistence de plusieurs espèces, que la réponse fonctionnelle (acquisition et utilisation) d'une espèce soit supérieure à une densité élevée d'une ressource et que celle de l'autre espèce soit supérieure à une faible densité de cette même ressource (Tilman *et al.*, 1982). De cette façon, la différentiation de niches implique une complémentarité fonctionnelle des espèces coexistentes (Loreau, 2004).

Les perturbations périodiques (p. ex. l'augmentation de la profondeur de la couche de mélange par le biais d'une tempête) peuvent également structurer les communautés de phytoplancton en interagissant avec la disponibilité des niches verticales et, par conséquent, affecter la diversité (Reynolds, Padisák et Sommer, 1993). Selon l'hypothèse de perturbation intermédiaire, la diversité atteint son maximum à des fréquences ou intensités intermédiaires de perturbation selon une relation parabolique (Connell, 1978). Ainsi, les masses d'eau présentant un niveau intermédiaire de perturbation ou d'hétérogénéité sont suffisamment stables pour permettre la formation d'agrégations de phytoplancton mais assez variables pour prévenir l'exclusion compétitive (Reynolds, 1993; Reynolds, Padisák et Sommer, 1993; Richerson, Armstrong et Goldman, 1970). Autrement dit, aucune espèce ne domine fortement à un niveau moyen de perturbation et, par conséquent, plusieurs espèces peuvent coexister (Reynolds, 1993; Reynolds, Padisák et Sommer, 1993). D'autre part, les colonnes d'eau bien mélangées présentent une hétérogénéité spatiale réduite avec des algues distribuées de façon plus homogène. Dans ces systèmes bien mélangés, la différenciation des niches est donc réduite et une diminution de la diversité est observée (Jäger, Diehl et Schmidt, 2008).

La diversité fonctionnelle et son importance

Les patrons de diversité du phytoplancton dans les lacs et leurs relations avec les gradients environnementaux se sont appuyés, à ce jour, principalement sur des analyses taxonomiques (Dodson, Arnott et Cottingham, 2000; Interlandi et Kilham, 2001; Smith *et al.*, 2005). Cependant, on peut s'attendre que les mesures de diversité fonctionnelle répondent mieux aux différents gradients spatiaux des ressources que les indices taxonomiques traditionnels. Les travaux précurseurs de R. Margalef ont tenté de prédire l'apparition de groupes fonctionnels de phytoplancton marin le long de gradients de nutriments et de turbulence (Margalef, 1978). Plus récemment, les études de Reynolds et collaborateurs ont utilisé des associations fonctionnelles de phytoplancton où les espèces ont été regroupées intuitivement par similarités morphologiques, physiologiques et écologiques, et liées à différents ensembles de conditions environnementales (Kruk *et al.*, 2002; Reynolds *et al.*, 2002). Ces associations fonctionnelles ont été plus sensibles aux facteurs environnementaux que les indices taxonomiques (Kruk *et al.*, 2002). Bien que l'on trouve une large distribution des espèces communes de phytoplancton dans les lacs, il est connu que sous certaines

conditions certaines espèces ou groupes d'espèces augmentent leur biomasse plus fortement que d'autres (Reynolds, 1998). Ces groupes d'espèces présentent ainsi une meilleure performance quand leurs attributs particuliers sont favorisés. Ces attributs ou traits fonctionnels peuvent être des caractéristiques morphologiques ou physiologiques d'un organisme qui influencent un ou plusieurs processus fonctionnels essentiels comme, entre autres, la croissance, la reproduction et la prise de nutriments (Weithoff, 2003). La diversité fonctionnelle, *via* une complémentarité dans l'utilisation des ressources, est importante pour le fonctionnement de l'écosystème, notamment la production primaire et la respiration (Hooper *et al.*, 2005; Loreau *et al.*, 2001).

Plusieurs méthodes ont été proposées pour mesurer la diversité fonctionnelle dans les communautés (Mason *et al.*, 2005; Petchey et Gaston, 2002; Walker, Kinzing et Langridge, 1999). Une méthode fréquemment utilisée pour mesurer la diversité fonctionnelle (en anglais FD, pour « functional diversity ») s'appuie sur un dendrogramme développé à partir d'une matrice de traits fonctionnels et d'espèces (Petchey et Gaston, 2002). Cette mesure de FD a été utilisée pour une grande variété de taxons (Blackburn *et al.*, 2005; Mouillot, Dumay et Tomasini, 2007; Petchey *et al.*, 2007), y compris le zooplancton (Barnett et Beisner, 2007; Barnett, Finlay et Beisner, 2007). Cependant, à notre connaissance, FD n'a pas encore été testé sur les communautés phytoplanctoniques.

Variations saisonnières dans la distribution verticale et la diversité du phytoplancton dans les lacs

La variabilité temporelle dans la forme et la profondeur de la thermocline estivale (p. ex. lors de sa formation au printemps et de sa destruction à l'automne) altère la distribution verticale des nutriments et de la lumière (Reynolds, 1989, 1990; Sommer *et al.*, 1986) et, par conséquent, la distribution et la composition du phytoplancton (Berger *et al.*, 2007; Sommer et al., 1986), tel que proposé par le modèle du « Plankton Ecology Group » (modèle PEG) (Sommer *et al.*, 1986). Pour résumer, lors de l'établissement de la stratification au printemps, la profondeur de la couche de mélange est réduite, avec pour conséquence, en particulier dans les lacs profonds, à l'exposition plus longue des algues dans la zone euphotique. Les flagellés dont la croissance est rapide, comme les cryptophytes, et les petites diatomées centriques dominent au printemps, permettant ainsi à la biomasse de la communauté phytoplanctonique

d'augmenter pour atteindre un maximum (Sommer *et al.*, 1986). La floraison printanière est généralement suivie d'une période de faible biomasse du phytoplancton, c'est-à-dire d'une phase durant laquelle l'eau est plus claire. Cette diminution de la biomasse des algues de petite taille quand la stratification devient plus stable et plus accentuée peut être attribuée à la fois à une diminution de la remontée des eaux profondes riches en nutriments vers l'épilimnion et au broutage intense par le zooplancton herbivore (Huppert, Blasius et Stone, 2002; Lampert *et al.*, 1986; Sarnelle, 1993; Sommer *et al.*, 1986). Lorsque la taille de la population de zooplancton est réduite et, par conséquent, que la pression du broutage est moins intense, et que des concentrations non limitantes de nutriments sont rétablies, la biomasse du phytoplancton augmente. À ce moment, la communauté phytoplanctonique devient plus riche et plus diversifiée fonctionnellement avec la présence des petites (ex. cryptophytes) et grandes (p. ex. les algues vertes coloniales) espèces (Sommer *et al.*, 1986). Lorsque l'été progresse, les algues vertes sont remplacées par une succession de grandes diatomées puis par les dinoflagellés et/ou les cyanophytes. À la fin de l'été ou au début de l'automne, une augmentation de la profondeur de mélange associée à la rupture de la stratification se traduit par un enrichissement en nutriments de l'épilimnion et une exposition réduite des algues à la lumière. Les communautés de phytoplancton sont alors dominées par des types fonctionnels adaptés aux conditions de mélange, comme les grandes formes unicellulaires ou filamenteuses. Ce type de phytoplancton peu susceptible d'être brouté par le zooplancton est fréquemment associé à une biomasse variable d'algues de petite taille plus sensibles au broutage (Sommer *et al.*, 1986).

Problématique et objectif général

Des changements dans la concentration de nutriments et de carbone organique dissous dans les lacs associés, par exemple, à la déforestation et à l'activité agricole, peuvent avoir un effet direct sur la biomasse et la composition du phytoplancton (Carpenter *et al.*, 1998; Reynolds, 1998) et/ou indirect *via* une modification de la structure physique de la colonne d'eau et, par conséquent de l'habitat disponible (Fee *et al.*, 1996; France, 1997). Bien que des relations entre la structure physique de la colonne d'eau avec la distribution, la composition et la diversité du phytoplancton aient été montrées expérimentalement et dans des études de terrain sur un ou quelques lacs (Clegg, Maberly et Jones, 2004; Jäger, Diehl et Schmidt,

2008; Ptacnik, Diehl et Berger, 2003; Reynolds, 1984; Viser *et al.*, 1996), il reste cependant à déterminer si les patrons pour un ensemble de lacs présentant différentes caractéristiques morphométriques et chimiques sont conformes à ces attentes. De plus, comme les associations fonctionnelles se sont révélées plus sensibles que les indices taxonomiques traditionnels aux différents gradients spatiaux de ressources (Kruk *et al.*, 2002), il reste également à vérifier si les relations avec la structure physique de la colonne d'eau seront plus fortes avec la diversité fonctionnelle qu'avec la diversité taxonomique. Cette thèse de doctorat vise ainsi à établir les patrons dans la distribution verticale et la diversité taxonomique et fonctionnelle du phytoplancton pour un ensemble de lacs du Sud du Québec (Canada) et à étudier leurs relations avec la structure physique de la colonne d'eau.

Objectifs spécifiques, hypothèses et démarche méthodologique des chapitres de thèse

De nombreuses études ont mis l'accent sur l'importance des variables morphométriques dans la prédiction de la forme et de la profondeur de la thermocline (Gorham et Boyce, 1989, Patalas, 1984). Cependant, d'autres études suggèrent que dans les lacs présentant une petite superficie (p. ex. <5 km^2, Fee *et al.*, 1996; et <12.5 km^2, Mazumder et Taylor, 1994) la transparence de l'eau est un facteur plus important que la morphométrie même du lac pour déterminer l'épaisseur de l'épilimnion. Du fait que la structure physique de la colonne d'eau d'un lac (définie par des gradients de lumière et de température) peut avoir une influence sur la distribution et la diversité du phytoplancton (Clegg, Maberly et Jones, 2007; Jäger, Diehl et Schmidt, 2008; Klausmeier et Litchman, 2001), les facteurs environnementaux qui influencent cette dernière ont été étudiés en premier lieu. Ainsi, à travers l'étude de 45 lacs du Sud du Québec (Canada) montrant des variations importantes de taille, de concentration d'éléments nutritifs et de couleur de l'eau, le premier objectif du premier chapitre est d'identifier les facteurs qui prédisent le mieux la structure de l'habitat pour le phytoplancton, où l'habitat est défini par : la pénétration de la lumière, la profondeur de la thermocline, l'hétérogénéité dans la distribution verticale de la température et la résistance thermique relative (RTR) au mélange de la colonne d'eau. Le second objectif de ce chapitre est de déterminer comment la structure physique de la colonne d'eau affecte la distribution de la biomasse du phytoplancton. La première hypothèse associée à cet objectif est que :

(H1) des couches plus définies de la biomasse du phytoplancton (caractérisées par un coefficient de variation verticale plus élevé) sont présentes dans les habitats plus hétérogènes (c'est-à-dire avec une plus grande hétérogénéité verticale de la température et/ou une plus grande RTR au mélange).

En fonction des besoins en ressources et de la capacité spécifique de déplacement dans la colonne d'eau des différents groupes de phytoplancton, la seconde hypothèse est que :
(H2) la distribution verticale (p. ex. la profondeur du maximum de biomasse et le coefficient de variation verticale) de chaque groupe de phytoplancton est affectée différemment par la structure de l'habitat.

Les groupes de phytoplancton examinés sont limités à ceux mesurables avec un spectrofluoromètre submersible (FluroProbe), qui permet la détection à très fine échelle spatiale (de l'ordre du centimètre) de la biomasse des cyanophytes, des algues brunes (diatomées, chrysophytes et dinoflagellés), des algues vertes (chlorophytes) et des cryptophytes (Gregor et Maršálek, 2004; Gregor *et al.*, 2005).

Afin de vérifier si les tendances observées sont robustes, des lacs de deux régions voisines du Sud du Québec présentant différentes caractéristiques sont étudiées. Les régions des Laurentides et de l'Estrie diffèrent par leur géologie, leur paysage environnant et la nature de leur COD coloré, avec une contribution du COD coloré au coefficient d'extinction de la lumière beaucoup plus élevée dans la région des Laurentides que dans l'Estrie (Prairie, Bird et Cole, 2002). D'autre part, les lacs des Laurentides présentent généralement des valeurs de fetch plus faibles et sont plus protégés du vent (Pinel-Alloul, Bourbonnais et Dutilleul, 1996; Prairie, Bird et Cole, 2002). Ainsi, les deux derniers objectifs du premier chapitre sont d'identifier les variables environnementales qui ont un effet sur la structure physique de la colonne d'eau dans les lacs de ces deux régions, puis de comparer leurs relations entre la distribution du phytoplancton et l'hétérogénéité physique de la colonne d'eau. Les hypothèses reliées à ces objectifs sont que :
(H3) la structure de l'habitat pour le phytoplancton (lumière, profondeur et forme de la thermocline et RTR au mélange) diffère entre les deux régions en raison de leurs différences dans leur environnement chimique et dans leurs variables morphométriques. Une plus faible pénétration de la lumière, une thermocline moins profonde et une plus forte hétérogénéité

verticale de la température sont attendues dans les lacs de la région des Laurentides étant donné que ces lacs sont plus riches en COD coloré et moins exposés au vent que les lacs de la région de l'Estrie;

et que :

(H4) les différences dans la distribution verticale du phytoplancton (la profondeur du maximum de biomasse et le coefficient de variation verticale) entre les lacs des deux régions sont attribuables à des différences dans la structure physique de leur colonne d'eau, avec des maxima de biomasse moins profonds et une distribution verticale du phytoplancton plus hétérogène dans les lacs de la région des Laurentides.

Suite à l'identification dans le premier chapitre des facteurs qui affectent la distribution du phytoplancton, le second chapitre vise à évaluer les patrons de diversité taxonomique et fonctionnelle dans les communautés de phytoplancton de plusieurs lacs au regard des facteurs environnementaux qui définissent la présence et la persistance des niches disponibles pour le phytoplancton. La première hypothèse reliée à cet objectif est que :

(H1) une diversité plus élevée du phytoplancton est observée dans les lacs qui présentent une structure verticale plus hétérogène (p. ex. des coefficients de variation verticale de la température plus élevés), ainsi que dans les lacs sujets au mélange par le vent (p. ex. les lacs qui présentent une RTR au mélange plus faible), ce qui empêche l'exclusion compétitive dans les niches.

La diversité du phytoplancton est mesurée par deux indices s'appuyant sur la taxonomie (la richesse en espèces et l'indice de Shannon) ainsi que par un indice de diversité fonctionnelle [FD calculé selon la méthode de Petchey et Gaston (2002)] afin de déterminer si les différentes mesures de diversité répondent de façon similaire à la structure de l'habitat. Parce que des associations fonctionnelles du phytoplancton ont été plus sensibles aux variations des facteurs environnementaux que les indices taxonomiques classiques (Kruk *et al.*, 2002), la seconde hypothèse est que :

(H2) les relations entre les variables environnementales et les mesures de diversité sont plus fortes [avec un coefficient de détermination (R^2) plus élevé] avec la diversité fonctionnelle qu'avec la diversité taxonomique.

Pour vérifier si les tendances observées sont robustes les lacs des Laurentides et de l'Estrie, sont comparés. Les hypothèses associées à cet objectif sont que :

(H3) les patrons dans la diversité du phytoplancton sont différents entre les deux régions;

et que :

(H4) ces différences dans les patrons de diversité du phytoplancton entre les deux régions sont attribuables aux différences dans leur environnement physique et chimique et dans leurs caractéristiques morphométriques des lacs. Une diversité plus élevée est attendue dans la région des Laurentides, où la distribution de la température est plus hétérogène.

Lors de variations dans la thermocline estivale, la lumière disponible pour le phytoplancton et la distribution verticale des nutriments dans la colonne d'eau sont modifiées et, par conséquent, la distribution et la composition du phytoplancton (Berger *et al.*, 2007; Sommer *et al.*, 1986). Il est également probable que les différents groupes de phytoplancton montrent des réponses distinctes. L'objectif du troisième chapitre est donc d'évaluer les tendances dans la distribution, la composition et la diversité dans les communautés de phytoplancton lors de variations dans la thermocline estivale. Les hypothèses pour ce chapitre sont que :

(H1) la distribution verticale de la biomasse de phytoplancton (p. ex. la profondeur du maximum de biomasse et le coefficient de variation verticale) varie avec la saison. Des maxima de biomasse plus profonds sont attendus au printemps quand la pénétration de la lumière et le mélange induit par le vent sont généralement plus élevés. À la mi-mi-été, quand la thermocline est bien établie et que la RTR au mélange par le vent est plus grande, une plus grande hétérogénéité dans la distribution du phytoplancton est attendue;

et que :

(H2) la distribution verticale (p. ex. la profondeur du maximum de biomasse et le coefficient de variation verticale) des groupes spectraux de phytoplancton répond différemment aux changements dans la structure de l'habitat lors des périodes examinées.

Du fait que des variations dans la structure physique de la colonne d'eau peuvent être accompagnées de changements dans la disponibilité des niches pour le phytoplancton (Clegg, Maberly et Jones, 2007; Reynolds, 1984), les dernières hypothèses associées à ce chapitre sont que :

(H3) des différences dans la diversité du phytoplancton sont observées lors de variations de la thermocline estivale. Une diversité du phytoplancton plus élevée est attendue dans la période avec une plus grande hétérogénéité verticale de la colonne d'eau, mais également quand les lacs sont sujets à du mélange induit par le vent;

et que :

(H4) les relations entre les variables environnementales et les indices de diversité sont plus fortes (p. ex. avec un R^2 plus élevé) avec la diversité fonctionnelle qu'avec la diversité taxonomique.

Afin d'atteindre cet objectif, 18 lacs du Sud du Québec (Canada) sont examinés lors de trois périodes distinctes : le printemps tardif, la mi-été et le début de l'automne. Ces lacs montrent des gradients prononcés dans la morphométrie, la productivité et la couleur de l'eau.

CHAPITRE I

ENVIRONMENTAL FACTORS CONTROLLING THE VERTICAL DISTRIBUTION OF PHYTOPLANKTON IN LAKES

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L'auteure principale de cet article, Maria Lorena Longhi, était responsable et a réalisé : l'échantillonnage de terrain, les analyses de laboratoire, les analyses de données, la recherche bibliographique et la rédaction de l'article. La co-auteure, Beatrix E. Beisner, en qualité de directrice de thèse de Maria Lorena Longhi, était responsable d'orienter et d'apporter ses commentaires dans toute la démarche ayant mené à cet article.

Observations from single lake and experimental studies predict that vertical habitat heterogeneity in lakes can influence phytoplankton community structure. We examined the nature of water column physical habitat structure (light penetration, thermocline depth and shape and relative thermal resistance to mixing), and in turn, how these structures influenced the distribution of bulk chlorophyll *a* and the biomass of several major phytoplankton groups across 45 lakes in eastern Canada, within two lake districts which varied in watershed geology and water chemistry. Across all lakes, more pronounced temperature gradients favoured the distribution of bulk phytoplankton into more defined layers. The depth at which peak chlorophyll *a* was observed was affected by temperature heterogeneity and environmental factors related to light penetration. Peak depths and vertical heterogeneity of the major phytoplankton groups were differentially related to epilimnetic water colour and total phosphorus concentration across all lakes. Further insight was gained by comparing the physical structure and phytoplankton responses in the two regions. Lakes from the Laurentians Region had less wind exposure, shallower thermoclines, but greater vertical temperature variability than lakes from the Eastern Townships Region. As a result, total and major phytoplankton group biomass showed more heterogeneous distributions in the Laurentians. The depth of peaks in total biomass and for the major phytoplankton groups was similar in both regions; the exception being a deeper chlorophyte maximum in the Eastern Townships Region, suggesting that there may be important differences between regions in the taxonomic composition of this group.

1.1 Introduction

Habitat heterogeneity in lakes plays a key role in controlling the abundance, distribution and diversity of phytoplankton (Clegg, Maberly and Jones, 2007; Klausmeier and Litchman, 2001; Reynolds, 1984). Heterogeneity in the water column can be represented by vertical gradients in temperature, light or nutrients. Pronounced environmental gradients should favour the distribution of phytoplankton in defined layers, that in their most obvious expression concentrate large proportions of algal biomass into surface blooms, deep chlorophyll maxima or benthic layers (Clegg, Maberly and Jones, 2007; Klausmeier and Litchman, 2001).

The intensity of light in the water column of lakes decreases exponentially with depth. Moreover, the wavelengths represented at depth vary with the spectral quality of the water (Kirk, 1994). Different phytoplankton groups have specialised pigments that allow absorption of particular parts of the light spectrum as well as at different light intensities (Falkowski and

Raven, 1997). Phytoplankton can therefore maximize light absorption by optimizing their depth in the water column, a behaviour which at the community level, can potentially allow for the coexistence of a number of species and promote phytoplankton diversity (Falkowski and Raven, 1997; Stomp *et al.*, 2004, 2007).

The summer thermocline in North Temperate lakes is another predominant physical factor likely to affect phytoplankton because it controls sedimentation losses and restricts the availability of nutrients and gasses (Fee, 1976; Reynolds, 1984). The effect of wind is largely related to the morphometric characteristics of a lake and the interplay of these factors affects the establishment and depth of the thermocline: generally, thermoclines are deeper for larger lake surface areas or wind fetch (Fee *et al.*, 1996; Patalas, 1984). The shape of the thermocline can also be a function of lake bathymetry because subsurface structure further affects current and turbulence mixing patterns (MacIntyre *et al.*, 1999). Since light is the principal source of heat to the water column, lake thermal structure (e.g. thermocline depth) is also affected by water transparency (Fee *et al.*, 1996; Houser, 2006; Snucins and Gunn, 2000). Light penetration is particularly reduced, as is the thickness of the epilimnion, when algal blooms occur (e.g. eutrophic lakes), or where there are high concentrations of coloured dissolved organic carbon (DOC) (e.g. dystrophic lakes) (Fee *et al.*, 1996; Mazumder *et al.*, 1990; Snucins and Gunn, 2000). Some studies have shown, however, that the effect of light (water transparency) better predicts thermocline depth in smaller lakes (Fee *et al.*, 1996; Mazumder and Taylor, 1994).

In response to the gradients of essential resources (i.e. light and nutrients) during the period of summer stratification phytoplankton groups are predicted to show differential vertical distributions as they optimize growth conditions according to their specific physiologies and motilities (Clegg, Maberly and Jones, 2007; Diehl, 2002; Klausmeier and Litchman, 2001). Peak biomass of different phytoplankton groups may be expected at different depths: diatoms near the metalimnion where colder, denser water can prevent their sinking (Reynolds, 1984), some cyanophytes which can modulate their position by buoyancy might form surface blooms (Reynolds, 1984; Visser *et al.*, 1996), whereas cryptophytes may peak in the metalimnion where their tolerance to low-light and their high-nutrient requirements are normally satisfied (Klaveness, 1988; Ptacnik, Diehl and Berger, 2003). Such

relationships between water column heterogeneity and phytoplankton group distribution have been demonstrated experimentally (Clegg, Maberly and Jones, 2004; Ptacnik, Diehl and Berger, 2003; see Reynolds, 1984 and references therein), and in field studies on a single or a few lakes (see Reynolds, 1984 and references therein; Viser *et al.*, 1996). However, it remains to be determined whether patterns across many lakes with different physical and chemical characteristics are consistent with these expectations, and whether lake districts with different underlying characteristics, such as water colour and wind exposure, show the same relationships.

The goal of this study was to determine how the physical structure of the water column influences the distribution of several major groups of phytoplankton across two lake districts. By examining lakes that vary dramatically across nutrient, colour and size gradients, we initially set out to identify lake factors that best predict proximate habitat structure for phytoplankton, where habitat is defined by: light penetration, thermocline depth, temperature heterogeneity and the relative thermal resistance to mixing of the water column. We then hypothesized (H1) that more defined layers of phytoplankton biomass (measured as a higher vertical coefficient of variation) would be found in more heterogeneous habitats (i.e. greater vertical temperature heterogeneity and/or higher relative thermal resistance to mixing). Based on the specific resource requirements and abilities of phytoplankton to move in the water column, we further hypothesized (H2) that the vertical distribution (e.g. depth of maximum biomass and coefficient of variation) of each phytoplankton group would be differentially affected by habitat structure. Phytoplankton groups examined were restricted to those measurable with a submersible spectrofluorometer to allow fine-scale detection of the distribution of: cyanophytes, brown microalgae (diatoms, chrysophytes and dinoflagellates), chlorophytes and cryptophytes.

In order to ensure that patterns observed were robust across districts of different types, lakes in two neighbouring areas of Southern Québec, Canada were studied. The Laurentians Region (LR) and the Eastern Townships Region (ETR) differ not only in their geology and surrounding landscape but also in the nature of their coloured DOC, with a much higher contribution of DOC to the light extinction coefficient in the LR than in the ETR (Prairie, Bird and Cole, 2002). In addition, lakes from the LR generally have lower wind fetch and are

more protected from wind (Pinel-Alloul, Bourbonnais and Dutilleul, 1996; Prairie, Bird and Cole, 2002). We further hypothesized (H3) therefore that phytoplankton habitat structure (light, thermocline depth and shape, and relative thermal resistance to mixing) would differ between the regions because of differences in the chemical environments and morphometric variables. We expected lower light penetration, shallower thermoclines and higher vertical heterogeneity of temperature in lakes from the LR since these lakes are more coloured and less wind exposed. Finally, we hypothesized (H4) that differences in phytoplankton vertical distribution (depth of maximum biomass and coefficient of variation) between regions would be attributable to differences in their physical environments, with shallower peak positions and higher vertical heterogeneity of phytoplankton expected in lakes from the LR.

1.2 Methods

1.2.1 Study sites and sampling

This study included a total of 45 lakes from two different regions of Southern Québec: the Eastern Townships Region or ETR (25 lakes) and the Laurentians Region or LR (20 lakes). A summary of the physical, chemical and biological characteristics of all lakes and for the two regions are shown in Table 1.1. Lakes from the ETR are located in a well-buffered calcareous region underlain by a sedimentary geology, whereas LR lakes are located on the southern part of the Canadian Shield underlain by gneiss-granitic bedrock covered by morainic soils. Lakes were chosen to span a wide range of physical and chemical characteristics (Table 1.1), from shallow to deep [maximum depth (Z_{max}): 4.2-84.8 m], oligotrophic to eutrophic [epilimnetic total phosphorus (TP): 5.22-47.98 $\mu g\ L^{-1}$] and low to moderate DOC (2.07-9.29 $mg\ L^{-1}$). Sampling was carried out once at the deepest point in each lake during the period of high summer stratification in July 2004 for 15 lakes in the ETR and in July 2005 for the other 30 lakes. Although the lakes were sampled in two different years, all samples were taken during the month of July at the peak of summer weather and stratification. To ensure that there was no effect of sampling year on the environmental factors, nor on the phytoplankton variables, we performed analyses of covariance (ANCOVAs, see Statistical Analyses section) with years as covariate (never a significant covariate).

Table 1.1
Physical, chemical and biological characteristics of all studied lakes and lakes from the two contrasted regions

	All lakes			Eastern Townships			Laurentians		
Variable	Min.[a]	Mean	Max.[b]	Min.[a]	Mean	Max.[b]	Min.[a]	Mean	Max.[b]
Maximum depth (m)	4.20	21.65	84.80	4.30	24.37	84.80	4.20	18.26	59.00
Fetch (km)	0.33	1.90	7.49	0.39	2.50	7.49	0.33	1.16	2.46
Epilimnetic total phosphorus ($\mu g\ L^{-1}$)	5.22	17.26	47.98	5.22	15.95	43.78	5.40	18.99	47.98
Dissolved organic carbon ($mg\ L^{-1}$)	2.07	5.63	9.29	2.27	5.54	8.83	2.07	5.75	9.29
Absorption at 440 nm (m^{-1})	0.00	1.46	3.92	0.00	1.35	3.34	0.00	1.61	3.92
Secchi depth (m)	1.25	3.97	9.50	1.25	4.07	9.50	1.50	3.85	8.50
Thermocline depth (m)	1.60	5.24	12.40	1.60	6.16	12.40	2.04	4.08	7.60
Coefficient of variation of the temperature	0.00	0.29	0.61	0.01	0.23	0.58	0.00	0.36	0.61
Relative thermal resistance to mixing	0.94	3.36	7.87	0.94	2.36	4.41	1.58	4.61	7.87
Mean chlorophyll *a* ($\mu g\ L^{-1}$)	0.37	3.39	15.34	0.37	3.44	15.34	0.43	2.41	7.86
Depth of maximum Chl *a* (m)	0.30	4.60	12.60	0.30	4.60	12.60	0.50	4.60	9.05
Coefficient of variation of Chl *a*	0.12	0.58	1.72	0.12	0.49	1.12	0.26	0.70	1.72

[a]Minimum value.
[b]Maximum value.

1.2.2 Physical structure of the water column

Four descriptors characterizing the physical structure of the water column were each used: water transparency, thermocline depth, coefficient of variation of the temperature profile and mean relative thermal resistance to mixing. Water transparency was measured with a Secchi disc (Secchi depth: Z_{Secchi}). Temperature profiles were recorded with a temperature sensor attached to a submersible spectrofluorometer (FluoroProbe, bbe-Moldaenke, Kiel, Germany) (accuracy: 0.1°C). For each lake, thermocline depth (Z_{thermo}) was defined as the depth at which the vertical temperature gradient was the greatest. With the exception of lakes Drolet, St Georges and Waterloo in the ETR, and Renaud and Walfred in the LR, all water bodies were stratified. For the unstratified lakes, the overall lake depth was used to estimate Z_{thermo}. Coefficient of variation of the temperature (CV temp.) was calculated as the standard deviation of the temperature profile divided by the mean over the photic zone. A higher value of CV temp. indicates a more heterogeneous temperature distribution. Photic zone depth was estimated as $2.79*Z_{Secchi}$ in each lake (Margalef, 1983).

Mean relative thermal resistance (RTR) to mixing was used to characterize the stability of the water column at the time of sampling. It was calculated over the photic zone as the average of density differences of all adjacent 10 cm layers relative to the density difference between water at 4° and 5°C according to the formula:

$$RTR = \overline{(\rho 2 - \rho 1) . 10^6 / 8},$$

where ρ_2 and ρ_1 are the densities (g cm^{-3}) at the bottom and the top, respectively, of the stratum being considered and RTR is measured in relative units (Birge, 1910).

1.2.3 Chemical measurements

Water samples for chemical analyses were collected at 0.5 m depth with a 2 L van Dorn bottle at the deep point in each lake. Within the same summer, TP and DOC values in epilimnetic and hypolimnetic waters were also measured in a subset of our lakes (unpublished results; S. Beauvais, Y. Prairie, P. del Giorgio for the ETR and R. Carignan for the LR) which allowed us to determine whether the hypothesized presence of a vertical nutrient gradient was a common feature in our lakes.

In the laboratory, TP was measured spectrophotometrically by the molybdenum blue method after persulfate digestion (Griesbach and Peters, 1991). DOC concentrations of filtered water samples (surfactant-free membrane filters) were measured after acidification (sulphuric acid 5%) followed by sodium persulfate oxidation using a 1010 TOC analyzer (O.I. Analytical, College Station, TX, USA). The absorption coefficient at 440 nm (A_{440}), used as a measure of water colour, was measured on filtered (Whatman GF/F) water samples with a 2 cm quartz cuvette (Cuthbert and del Giorgio, 1992) as:

$$A_{440} = 2.303 \text{ . (absorbance at 440 nm / 0.02 m)}$$

1.2.4 Phytoplankton measurements

Vertical profiles of total and major taxonomic group biomass were measured *in situ* using the FluoroProbe. The instrument measures fluorometrically the concentration of chlorophyll *a* (Chl *a*) in µg L^{-1} for four major spectral groups of phytoplankton, representing broadly the taxonomic classes of diatoms + dinoflagellates + chrysophytes (called "BROWN"), chlorophytes ("GREEN"), cyanophytes containing phycocyanin ("CYANO") and cryptophytes ("CRYPTO"). Fluorescence of coloured dissolved organic matter ("yellow substances") was subtracted from original fluorescence measurements by using a UV-B excitation source which allows the differentiation between algal fluorescence and fluorescence of "yellow substances" (Beutler *et al.*, 2002). Characteristic examples of FluoroProbe profiles from each region can be found in Supplementary data, Appendix A. Biomass measured for each phytoplankton group corresponds well with HPLC analysis (Beutler *et al.*, 2002), with traditional chlorophyll *a* extraction techniques (Gregor and Maršálek, 2004) and with taxonomic analyses (Gregor *et al.*, 2005). In our study, duplicate Chl *a* samples were taken at three depths (0.5, 2 and 3 m) for verification of the total biomass measured with the FluoroProbe in two of the lakes studied (mesotrophic Lovering and eutrophic Trois Lacs). Chl *a* estimated by ethanol extraction and measurements on a spectrophotometer (Wetzel and Likens, 1991; Wintermans and de Mots, 1965) were well correlated (Pearson's $r > 0.90$, $P < 0.0001$, $n = 6$, calculated using the three depths together) with values obtained using the FluoroProbe (difference of less than ± 0.2 µg L^{-1} in Lovering and ± 3 µg L^{-1} in Trois Lacs). In addition, mean relative biomass of each spectral group calculated from the FluoroProbe and from the microscope analyses in the above-mentioned

lakes was not significantly different (t-tests; BROWN: t = -1.06, P = 0.2047; GREEN: t = -0.6, P = 0.328; CRYPTO: t = 1.08, P = 0.1959; CYANO: t = 0.00, P = 0.5). FluoroProbe profiles were obtained by starting at the lake surface and taking readings at ~ 1 cm intervals. To avoid variability at the centimetre scale in the measurements, we standardized the profiles by taking the average value of every 10 cm interval (7 to 10 data points per interval). Mean total phytoplankton biomass and average biomass of the four spectral groups were measured from the FluroProbe profiles over the photic zone. Depth of maximum biomass was defined as the depth at which the biomass was the greatest (total Chl *a* or by spectral group). When no clear single peak was observed (i.e. a relatively homogenous distribution of biomass), we used the depth at which the shallowest distinctive peak in biomass was observed. Vertical heterogeneity of biomass was estimated as the coefficient of variation (CV) of observed values over the photic zone. Lower values of CV of biomass suggest a more uniform photic zone distribution of the phytoplankton while a higher CV indicate a more heterogeneous distribution.

1.2.5 Statistical analyses

Differences between regions (ETR versus LR) in mean values for habitat structure (light penetration, thermocline depth, shape and relative thermal resistance to mixing) and phytoplankton vertical distribution (depth of maximum biomass and CV for total phytoplankton and each spectral group) were tested using Student's t-test.

ANCOVAs with regions as covariates (after checking for effects of sampling year) were used to identify and compare factors that accounted for the greatest variation between lakes in their physical properties as well as in the phytoplankton variables (i.e. depth of maximum Chl *a* and CV of Chl *a*) from the two regions. For the light-related habitat structure variable, Z_{Secchi}, the independent variables tested for were TP, A_{440} and Chl a_{mean}, all of which can potentially influence light penetration in lakes. To characterize the physical habitat related to temperature (Z_{thermo}, CV temp. and RTR), the independent variables were those related to lake morphometry (i.e. Z_{mean}, Z_{max} and fetch), chemistry (i.e. TP, A_{440} and Chl a_{mean}) and light (Z_{Secchi}). Phytoplankton distribution was characterized in ANCOVA by selecting amongst all habitat-related variables (Z_{Secchi}, Z_{thermo}, CV temp., RTR, as well as the lake morphometric and chemical variables).

Relationships between environmental variables and phytoplankton spectral groups in all studied lakes were analyzed using redundancy analysis (RDA). All variables were centred and standardized prior to ordination. Significant predictor variables were determined using forward selection and significance was assessed with Monte-Carlo permutation (999 permutations). Multivariate analyses of covariance (MANCOVA) were used to compare regressions between environmental variables and phytoplankton spectral groups from the two contrasted regions. Independent variables used were the same as for the ANCOVAs. RDA was performed using CANOCO version 4.5 (ter Braak, 1990) and the other statistical tests were carried out using JMP 8.0 (SAS Institute Inc. 2008) at $\alpha = 0.05$ level of significance. Variables with non-normal distributions were log-transformed prior to analysis and prior selection of independent variables was made to exclude those that had correlations of $> \pm 0.75$.

1.3 Results

1.3.1 Phytoplankton habitat characterization

1.3.1.1 Vertical patterns of total phosphorus and dissolved organic carbon

We compared epi- and hypolimnetic measurements of TP and DOC in a subset of the studied lakes (14 lakes from the ETR and 4 lakes from the LR; see Supplementary data, Appendix B). TP was higher in the hypolimnion than in the epilimnion for all lakes in the LR and for most lakes in the ETR. However, some deeper oligo-mesotrophic lakes from the ETR showed the opposite pattern (Lakes Bowker, Lovering, Orford, Stukely and the more eutrophic lake Brome). The difference in TP between the two layers decreased with increasing lake depth ($y = 4.5276 - 0.1043x$, $P = 0.0208$, $R^2_{adj.} = 0.25$), with shallow eutrophic lakes showing the largest difference in TP concentrations between layers. DOC was generally higher in the epilimnion than in the hypolimnion, with the exception of the shallow well mixed eutrophic lakes St. Georges and Waterloo (ETR), which showed higher DOC values in the hypolimnion.

1.3.1.2 Water transparency

Water transparency (Z_{Secchi}) varied widely across all lakes, from 1.25 m to 9.5 m (Table 1.1). Mean Z_{Secchi} was slightly greater, but not significantly so, in lakes from the ETR than from the LR (Student's *t*-test: t = -0.41, P = 0.3423, df = 43). From the ANCOVA, Z_{Secchi} in all study lakes was negatively related to both mean Chl *a* (Chl a_{mean}) and epilimnetic absorption at 440 nm (A_{440}), but there were no significant differences between regions in this relationship ($R^2_{adj.}$ = 0.64, Table 1.2).

1.3.1.3 Temperature related variables

Summer thermocline depth in all lakes varied from 1.6 to 12.4 m (Table 1.1) and mean Z_{thermo} was significantly deeper in lakes from the ETR than from the LR (t = -3.94, P = 0.0002, df = 43). Z_{thermo} in all sampled lakes was deeper in those with greater light penetration and higher fetch (Table 1.2). In addition, the ANCOVA showed that for this relationship, the contrasted regions had similar slopes but significantly different intercepts ($R^2_{adj.}$ = 0.65, Table 1.2), being higher in the ETR.

The coefficient of variation in temperature (CV temp.) calculated for the photic zone in all lakes ranged between 0 and 0.61 (Table 1.1), with significantly lower mean values in the ETR than in the LR (t = 2.73, P = 0.0046, df = 43). CV temp. in all lakes was significantly related to morphometric variables irrespective of region (ANCOVA, R^2_{adj} = 0.40). CV temp. was positively related to maximum lake depth and negatively to lake fetch (Table 1.2).

Mean relative thermal resistance (RTR) to mixing at the time of sampling in all lakes varied from 0.94 to 7.87 (Table 1.1) with values significantly greater in lakes from the LR than from the ETR (t = 5.12, P < 0.0001, df = 43). The ANCOVA suggested that RTR was positively related to light absorption at 440 nm. Also, the intercepts were significantly higher in the LR ($R^2_{adj.}$ = 0.46, Table 1.2).

Table 1.2

Results of ANCOVAs between phytoplankton habitat structure-related variables [Secchi depth (Z_{Secchi}), thermocline depth (Z_{thermo}), coefficient of variation of the temperature (CV temp.) and the mean relative thermal resistance (RTR) to mixing] and the environmental variables testing for differences in the Eastern Townships and Laurentians regions

	Coefficient (SE.)	*P*-value	$P_{overall}$	$R^2_{adj.}$
$Log_{10}Z_{Secchi}$				
Constant	0.6855 (0.0269)	<0.0001	<0.0001	0.64
Log_{10}Chl a_{mean}	-0.3470 (0.0580)	<0.0001		
$Log_{10}A_{440}$	-0.2838 (0.0521)	<0.0001		
$Log_{10}Z_{thermo}$				
Constant	-0.1838 (0.1513)	0.2314	<0.0001	0.65
$Log_{10}Z_{Secchi}$	0.4395 (0.0820)	<0.0001		
Log_{10}Fetch	0.1972 (0.0489)	0.0002		
Region	0.0608 (0.0167)	0.0008		
Log_{10}CV temp.				
Constant	-0.3910 (0.5368)	0.4704	<0.0001	0.40
$Log_{10}Z_{max}$	1.1439 (0.2047)	<0.0001		
Log_{10}Fetch	-0.5417 (0.1943)	0.0079		
Log_{10}RTR				
Constant	0.4617 (0.0290)	<0.0001	<0.0001	0.46
$Log_{10}A_{440}$	0.2290 (0.0786)	0.0060		
Region	-0.1393 (0.0286)	<0.0001		

Independent variables tested for Z_{Secchi} were epilimnetic total phosphorus, absorption at 440 nm (A_{440}) and chlorophyll *a* mean (Chl a_{mean}) and for the other regressions additional variables included mean and maximum depth (Z_{mean} and Z_{max}), fetch and Z_{Secchi}. All variables were log_{10} transformed. Only significant relationships ($P < 0.05$) were included. SE: standard error.

1.3.2 Phytoplankton distribution

1.3.2.1 Vertical structure of the total phytoplankton biomass

Single peaks in total Chl *a* were observed in 34 lakes, seven lakes had a second peak and four lakes showed no clear peak. The depth of maximum Chl *a* in all sampled lakes was widely variable, ranging from as shallow as 0.3 m to as deep as 12.6 m (Table 1.1). Mean depths did not differ by region (t = -0.003, P = 0.4988, df = 43). Depth of Chl a_{max} was positively related to the CV temp. and negatively to TP concentrations and absorption at 440 nm (Fig. 1.1) ($R^2_{adj.}$ = 0.73, Table 1.3). Moreover, the ANCOVA showed a statistically significant difference between regions in the relationships between depth of Chl a_{max} and Z_{thermo}. Comparing the slopes of the log-log relationships between these two variables indicated that with increasing Z_{thermo}, changes in depth of the Chl a_{max} were faster in the LR (slope: 1.51) than in the ETR (slope: 0.66).

CV of total phytoplankton biomass in all lakes ranged between 0.12 and 1.72 (Table 1.1) with mean values significantly lower in the ETR than the LR (t = 2.16, P = 0.0188, df = 43). CV of Chl *a* in all lakes sampled was positively related to both CV temp. and RTR (Fig. 1.2), and similar relationships held in the two regions (ANCOVA, $R^2_{adj.}$ = 0.47, Table 1.3).

1.3.2.2 Vertical structure of the different phytoplankton groups

In all lakes, as well in the two contrasted regions, the GREENs showed the shallowest maximum biomass (mean: 1.93, in all sampled lakes), whereas the BROWNs and CRYPTOs showed the deepest maxima (mean: 4.07 and 4.66, respectively) (Fig. 1.3A). Maximum biomass of CYANOs and BROWNs was shallower in lakes from the ETR than from the LR, whereas the opposite was observed for the GREEN and CRYPTO groups (Fig. 1.3A), although differences between regions were statistically significant only for the GREENS (GREEN: t = -2.02, P = 0.0269, df = 43; CYANO: t = 0.55, P = 0.2922, df = 43; BROWN: t = 0.83, P = 0.2042, df = 43; CRYPTO: t = -0.49, P = 0.3138, df = 43). Results of the RDA between the maximum biomass depths of the phytoplankton spectral groups and the environmental factors for all lakes showed that absorption at 440 nm was the only significant environmental factor (Fig. 1.4A); the depth of maximum CYANO biomass increasing with A_{440} and an opposite pattern in the BROWN and CRYPTO groups. No significant differences

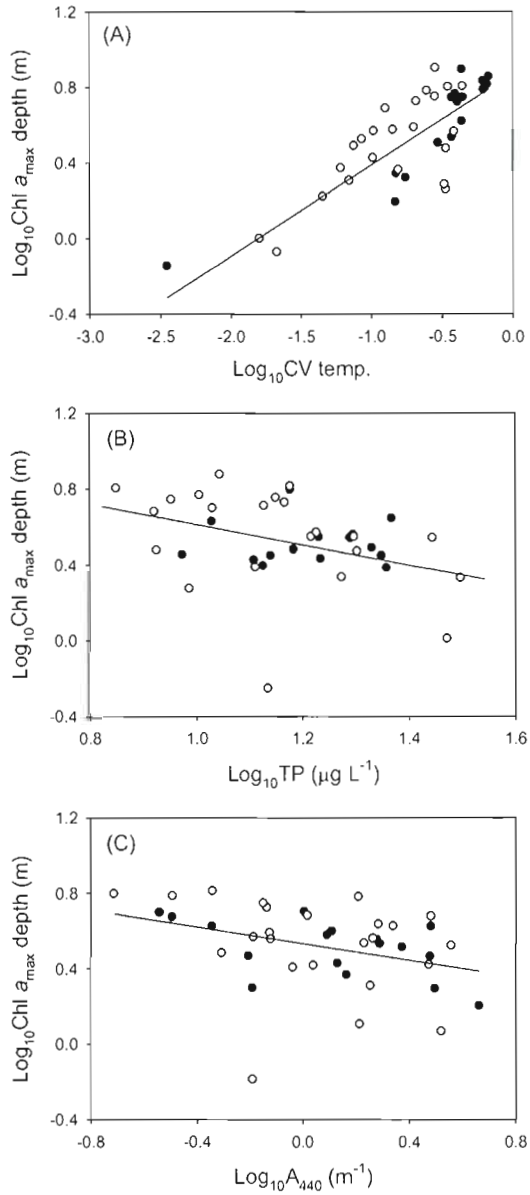

Fig. 1.1. Partial regression plots from a model relating the depth of maximum chlorophyll *a* (Chl a_{max} depth) to (A) coefficient of variation of the temperature (CV temp.), (B) epilimnetic total phosphorus (TP) and (C) absorption at 440 nm (A_{440}) for all studied lakes from the Eastern Townships (open circles) and Laurentians (solid circles) regions. All variables were $\log_{10}$ transformed.

Table 1.3

Results of ANCOVAs between phytoplankton distribution-related variables [depth of maximum Chl *a* (Chl a_{max} depth) and the coefficient of variation of the Chl *a* (CV Chl *a*)], and the environmental variables testing for differences in the Eastern Townships and Laurentians regions

	Coefficient (SE.)	*P*-value	$P_{overall}$	$R^2_{adj.}$
Log_{10}Chl a_{max} depth				
Constant	1.5638 (0.2037)	<0.0001	<0.0001	0.73
Log_{10}CV temp.	0.4819 (0.0694)	<0.0001		
Log_{10}TP	-0.5339 (0.1808)	0.0055		
$Log_{10}A_{440}$	-0.2209 (0.0968)	0.0286		
Region*$Log_{10}Z_{thermo}$	-0.5549 (0.2076)	0.0112		
Log_{10}CV Chl *a*				
Constant	-0.2451 (0.0962)	0.0146	<0.0001	0.47
Log_{10}CV temp.	0.2979 (0.0649)	<0.0001		
Log_{10}RTR	0.3050 (0.1362)	0.0305		

Independent variables tested were mean and maximum depth, fetch, epilimnetic total phosphorus (TP), absorption at 440 nm (A_{440}), Secchi depth (Z_{Secchi}), thermocline depth (Z_{thermo}), coefficient of variation of the temperature (CV temp.) and mean relative thermal resistance (RTR) to mixing. All variables were log_{10} transformed. Only significant relationships ($P < 0.05$) were included. SE: standard error.

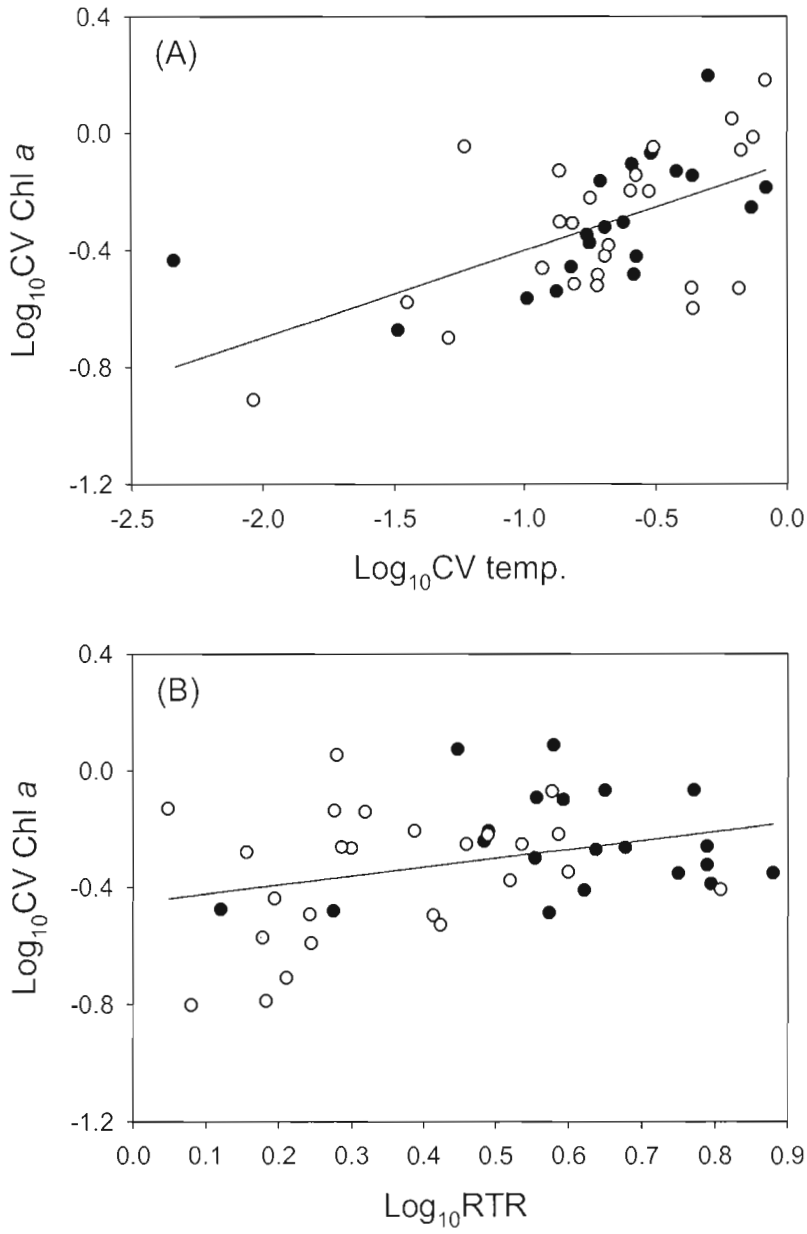

Fig. 1.2. Partial regression plots from a model relating the coefficient of variation of chlorophyll *a* (CV Chl *a*) to (A) CV of the temperature (CV temp.) and (B) mean relative thermal resistance (RTR) to mixing for all studied lakes from the Eastern Townships (open circles) and Laurentians (solid circles) regions. All variables were $\log_{10}$ transformed.

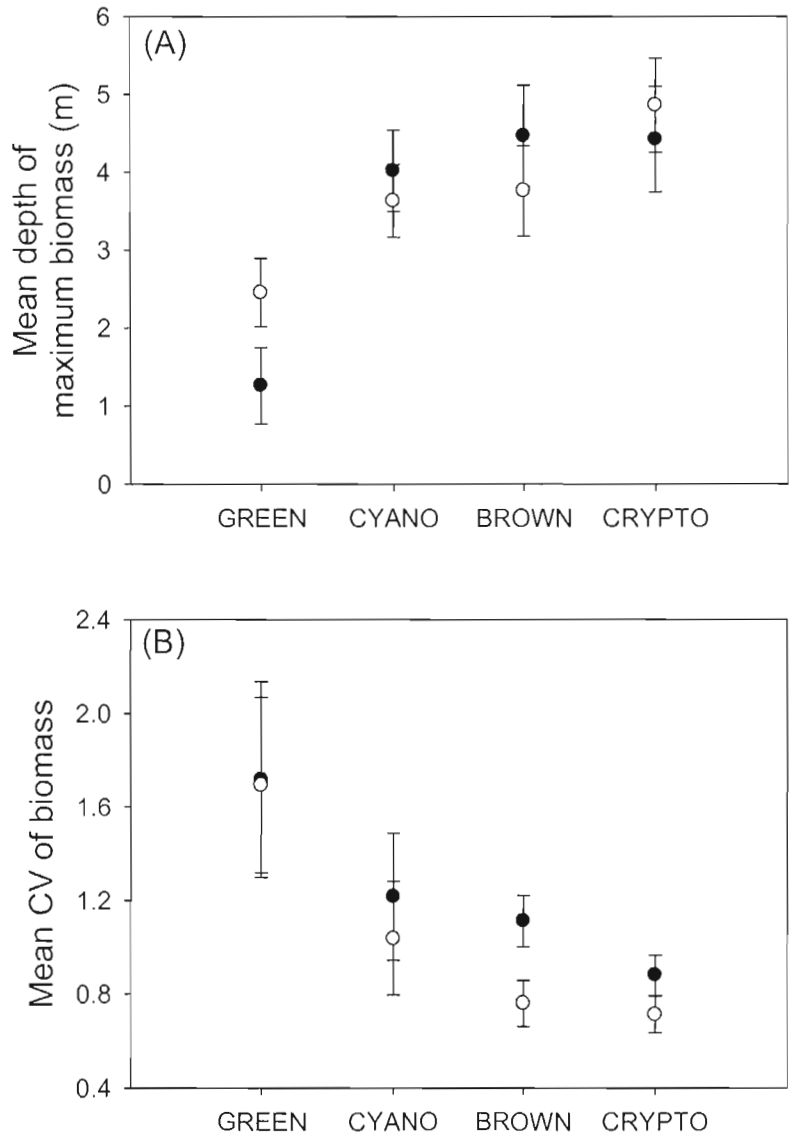

Fig. 1.3. Mean values of the (A) maximum biomass depth and (B) coefficient of variation (CV) of biomass of the different phytoplankton groups (GREEN, CYANO, BROWN and CRYPTO) of the two contrasted regions, Eastern Townships (open circles) and Laurentians (solid circles).

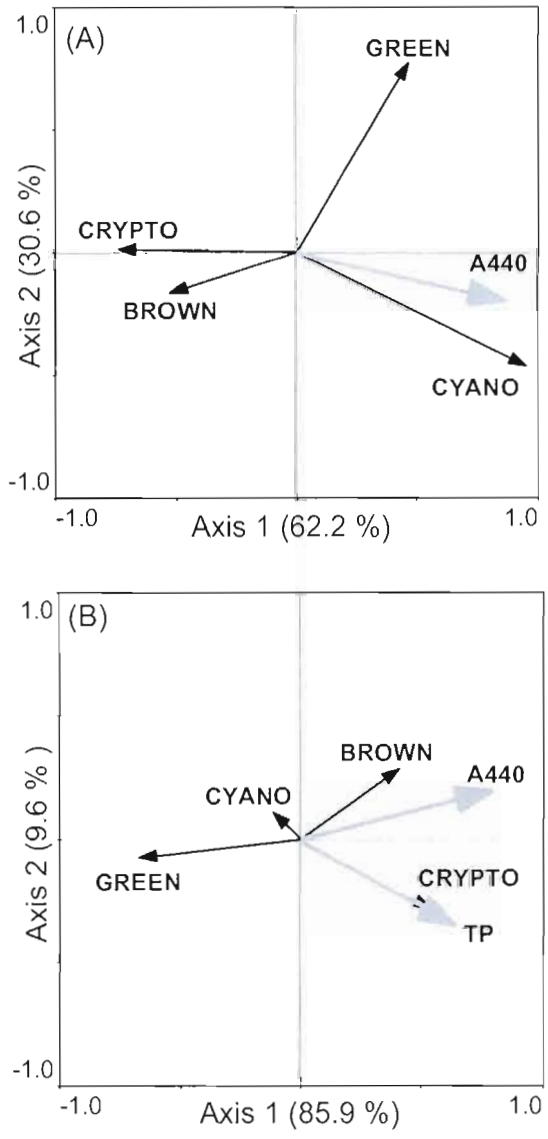

Fig. 1.4. Ordination biplots for the redundancy analysis of the (A) depth of maximum biomass and the (B) coefficient of variation of the biomass from the different phytoplankton groups and environmental variables for all studied lakes. Black arrows represent the phytoplankton groups and grey arrows represent the significant environmental factors that were selected by the RDA. Independent variables tested were mean and maximum depth, fetch, epilimnetic total phosphorus (TP), absorption at 440 nm (A_{440}), Secchi depth, thermocline depth, coefficient of variation of the temperature and mean relative thermal resistance to mixing.

between regions were found for the relationships between depth of maximum biomass of all four phytoplankton groups and the environmental variables (MANCOVA whole model: Wilks' λ app. $F = 0.89$, $P = 0.6578$).

Heterogeneity in the water column biomass distribution was higher in the GREENs (mean CV= 1.70) and lower in the BROWN and CRYPTO groups (mean CV= 0.92 and 0.79, respectively) (Fig. 1.3B). Biomass CV of the GREENs was similar in the two regions (Fig. 1.3B, $t = 0.04$, $P = 0.4828$). For the other three groups, CVs were lower in lakes from the ETR than from the LR but only significantly so for BROWNs (Fig. 1.3B, CYANO: $t = 0.50$, $P = 0.3085$, df = 43; BROWN: $t = 2.39$, $P = 0.0107$, df = 43; CRYPTO: $t = 1.46$, $P = 0.0757$, df = 43). An increase in A_{440} and TP concentration was related to greater vertical heterogeneity in the CRYPTO and BROWN groups, and to less variation in the GREENs (RDA; Fig. 1.4B). The relationships were not statistically different between regions (MANCOVA whole model: Wilks' λ app. $F = 1.90$, $P = 0.0104$).

1.4 Discussion

1.4.1 Habitat heterogeneity across all lakes

The main physical factors affecting phytoplankton vertical distribution in lakes are thought to be underwater light gradients and thermal stratification which can influence access to nutrient resources (Klausmeier and Litchman, 2001; Reynolds, 1984). In the majority of a substet of our lakes, we did observe that nutrient levels (TP) were greater in hypolimnetic waters than in epilimnetic ones, suggesting that a vertical gradient in nutrient resources is indeed present. Our initial goal was to establish observed relationships for the various potential driving factors of lake light and thermal structure, with the eventual goal of understanding how these might be important for bulk phytoplankton and spectral group vertical distribution. Overall, we found that darker lakes with more stained waters have more stable water columns and, where turbidity might also be present, they have shallower thermoclines as well. Lakes have deeper thermoclines and lower vertical variation in temperature where access by wind (fetch) is greater.

Light penetration across the whole suite of lakes in our study was highly variable, but declined with increases in both turbidity and water colour, as observed in previous studies

(Fee *et al.*, 1996; Mazumder *et al.*, 1990). Fee *et al.* (1996) found a tighter relationship between water transparency and DOC than with Chl *a* concentration in Canadian Shield lakes. In our lakes, both variables were nearly equally important in determining Z_{Secchi}.

We characterized the structure of thermal stratification using three measures: thermocline depth, vertical temperature variation and the relative thermal resistance to mixing. Overall, these thermal measures were most significantly affected by factors that influence wind access to the lake surface and the penetration of solar radiation, with some variation in the actual factor that was significant for each thermal measure. The first structural measure, thermocline depth, was observed to be deeper with increasing wind fetch and greater penetration of solar radiation; in both cases, phenomena which would distribute heat to greater depths. However, water transparency likely plays a more important role than mixing in high summer, when the thermocline is already well established. In small lakes, previous studies have similarly shown that water transparency best predicts thermocline depth [area < 5 km^2 (Fee *et al.*, 1996) and < 12.5 km^2 (Mazumder and Taylor, 1994)] and this likely applies to our study as well because only 5 of the 45 lakes were larger than 5 km^2. The second thermal structure measure, the vertical variation in temperature over the photic zone, was related only to morphometric variables, being lower in shallow lakes with larger fetch. In large, shallow lakes, because the water column is more easily mixed, temperature in the photic zone is more homogenous. The final measure used, the relative thermal resistance to mixing was positively related only to water colour across all of our lakes. RTR reflects the susceptibility of the entire water column to wind mixing, and thereby the potential for introducing hypolimnetic water and nutrients into the epilimnion, in our case, in high summer. As light absorption by coloured DOC increases, ultraviolet, and especially visible radiation, play an increasing role in warming the epilimnion (Calplanne and Laurion, 2008). Thus, more solar energy is retained and converted to heat at the surface of coloured lakes, all the while heating is reduced in hypolimnetic waters (Dillon *et al.*, 2003; Snucins and Gunn, 2000). The resulting increased temperature difference between the surface and deep layers yields a larger resistance to mixing of the water column in coloured lakes.

1.4.2 Phytoplankton vertical distribution across all lakes

The main goal of our study was to establish how fine scale phytoplankton distribution is related to vertical habitat heterogeneity (measured as light and thermal characteristics). This was done for both the entire phytoplankton community (bulk Chl *a*) as well as for four major spectral groups (GREEN, CYANO, BROWN and CRYPTO). We expected greater variation in phytoplankton spatial distribution in more heterogeneous habitats (those with higher RTR and CV temp.) with the spectral groups differentially affected by habitat structure.

The depth at which peaks in the bulk phytoplankton biomass was observed was related to both thermal stratification and water transparency factors. Notably, there was a great deal of variation in Chl *a* peak depths (from <1 m to 12.6 m). Previous experimental and theoretical work has shown that the thermal structure of the water column should influence phytoplankton biomass and vertical distribution by affecting the average light environment, nutrient availability and cell sedimentation loss (Diehl, 2002; Diehl *et al.*, 2002; Reynolds, 1984). We found deeper biomass maxima in lakes with greater temperature heterogeneity. Moreover, the position of maximum biomass was shallower in more turbid and coloured (high epilimnetic TP and A_{440}) lakes. TP provides an estimate of primary production (standing crop) in our lakes since there was a significant positive correlation between TP and phytoplankton biomass ($r^2 = 0.67$). Light absorbance and scattering by phytoplankton likely promoted light attenuation with depth, thereby indirectly affecting phytoplankton peak depth. Shallower accumulation of phytoplankton biomass with increasingly coloured DOC has also been reported from an experimental manipulation (Christensen *et al.*, 1996).

Our results support H1, which predicted greater variation in phytoplankton biomass in more heterogeneous habitats. Pronounced vertical temperature gradients favoured the distribution of bulk phytoplankton into more defined layers: greater variability in vertical biomass distribution in more stable lakes (high RTR) with a more heterogeneous temperature structure (high CV temp.). Weak wind mixing in lakes associated with marked vertical gradients in essential resources (such as light and nutrients) is predicted from theory to be associated with a more heterogeneous vertical distribution of phytoplankton (Klausmeier and Litchman, 2001).

The peak positions and heterogeneity of individual spectral groups of phytoplankton were differentially affected by habitat structure factors, as hypothesized in H2. We detected biomass peaks of several major phytoplankton groups in very thin layers (e.g. $\leq$ 1 m) using the FluoroProbe. Such peaks are difficult to observe with standard discrete sampling methods (Gregor *et al.*, 2005). Unlike the response of total phytoplankton variability to the thermal structure of the water column, at the spectral group level, vertical variation was related mainly to epilimnetic water colour and TP concentration with idiosyncratic responses by group. Since phytoplankton spectral groups measured with the FluoroProbe are discriminated by their specific composition of photosynthetic antenna pigments (Beutler *et al.*, 2002), it is not surprising that these groups could demonstrate differences in their responses to factors affecting the vertical gradient of light in the water column.

The first spectral group, the chlorophytes (GREENs) showed the shallowest average peak depth and the most heterogeneous distribution of all groups. Its heterogeneity was greatest in lakes with clear, unproductive waters. Chlorophytes tend to saturate photosynthesis at higher irradiance than other microalgal classes and consequently, can tolerate very high light levels (Richardson, Beardall and Raven, 1983), such as those found near the surface of the lakes. Cryptophytes (CRYPTOs), on the other hand, showed the deepest maxima and lowest heterogeneity in biomass distribution of the four spectral groups. The depth of maximum biomass of Cryptophytes is frequently found in the metalimnion of stratified lakes, as we also observed, where their low light and high nutrients requirements are both satisfied (Graham and Wilcox, 2000; Klaveness, 1988; Ptacnik, Diehl and Berger, 2003). Furthermore, the observed significant light climate effects on peak values and heterogeneity of the CRYPTOs could reflect the preference of this group for low-light environments (Graham and Wilcox, 2000; Klaveness, 1988), as well as its ability to select, by active motility, a favourable position in the water column (Clegg, Maberly and Jones, 2007). These characteristics likely confer a competitive advantage to cryptophytes in highly coloured (high DOC), low-light environments (Klug and Cottingham, 2001).

The most diverse spectral group, the BROWNs showed relatively deep maxima and low biomass heterogeneity in the water column. As for CRYPTO, the deeper peaks and the greater variation in vertical biomass distribution of the BROWNs were found in lakes with

high epilimnetic colour and TP. The interpretation of these relationships is complex because of the mixed nature of this spectral group. In our lakes, the BROWN group was mainly composed of diatoms and chrysophytes, while dinoflagellates contributed to only a small fraction of this group's biomass (microscope counts; data not shown). Since diatoms tend to sink, their peaks are expected to be near the metalimnion in well-stratified, relatively calm waters, where a denser layer of water can slow their sinking and favour biomass accumulation (Reynolds, 1984). Moreover, diatoms tended to dominate under low-light conditions (Jäger, Diehl and Schmidt, 2008; Litchman, 1998). Chrysophyte ecology is quite different since they show affinities for moderate light levels and their flagella allow them to select and maintain favourable positions throughout the water column (Clegg, Maberly and Jones, 2007). The fact that we mostly detected the BROWNs in metalimnetic peaks suggests that these peaks are probably dominated by diatoms, while the chrysophytes are less abundant and/or more diffusely distributed, without major peaks. However, to determine whether this is unequivocally the case, taxonomic sampling at peak depths as well as throughout the water column is required.

The final measured spectral group, the cyanobacteria (CYANOs) showed intermediate mean values of peak position and heterogeneity. This group was especially well represented in shallow lakes which usually have high TP, particularly in the ETR. The ecology of this group is also varied. Although many cyanobacteria have low light-energy requirements, as is also the case with diatoms and cryptophytes, some species can tolerate higher light levels such as those found near the surface of clear waters (see refs. in Dokulil and Teubner, 2000). Thus, changes in CYANO taxonomic composition with different light tolerances could explain the positive relationship observed between peak depth of cyanobacteria and water colour.

Zooplankton grazing, a factor not considered in this study, might also be important in affecting phytoplankton distribution and may explain some of the unaccounted variation in our statistical relationships. In a subset of our ETR lakes, zooplankton composition was shown to change along a cross-lake gradient of TP (Barnett and Beisner, 2007; Barnett, Finlay, and Beisner, 2007). Eutrophic lakes were mainly dominated by smaller, less competitive herbivorous crustacean zooplankton species, whereas oligotrophic lakes were

more likely to consist of a diversity of zooplankton body sizes and trophic groups, feeding mainly on chrysophytes and diatoms (Barnett and Beisner, 2007; Barnett, Finlay, and Beisner, 2007). Such variety of feeding and behavioural (e.g. diel vertical migration) strategies amongst the herbivores could potentially affect the size and vertical position of the peaks of the different phytoplankton groups. For example, large zooplankton migration has been found to support greater phytoplankton biomass accompanied by a change in the epilimnetic composition of the phytoplankton community towards smaller, more edible algae (Reichwaldt and Stibor, 2005). The role of the top-down effects of zooplankton in driving fine-scale vertical structure in the phytoplankton remains largely unexplored and requires further study.

1.4.3 Contrasting lake districts

Further insight into the factors affecting vertical habitat structure as well as phytoplankton distribution was gained by contrasting the two regions which differ in their bedrock geology and surrounding landscape, as well as in their lake morphometry (Pinel-Alloul, Bourbonnais and Dutilleul, 1996; Prairie, Bird and Cole, 2002). Differences in these factors were predicted to influence the habitat structure for phytoplankton and thereby their distributions. In characterizing each lake district, we found that lakes in the ETR were generally larger, having both greater wind fetches and higher maximum depths than lakes from the LR. Contrary to expectation, mean light penetration (Z_{secchi}), as well as the relationships with the statistically selected environmental factors (mean Chl *a* and absorption at 440 nm) was quite similar between the two regions. Thus, although the mean and range of bulk phytoplankton biomass were higher in the ETR than in the LR, these differences were not reflected in light penetration. A previous study estimated that the contribution of DOC to the light extinction coefficient was more than twice in the LR over ETR lakes, and suggested that this was probably related to a more refractory nature of DOC in the LR (Prairie, Bird and Cole, 2002). However, in our set of lakes, average absorption at 440 nm (a measure of water colour related to DOC absorption; Cuthbert and del Giorgio, 1992) was only slightly higher in the LR than in the ETR. We attribute the difference from previous work to variation in the set of sampled lakes, as well as potentially, in sampling years.

Variables describing the phytoplankton habitat structure (e.g. thermocline depth and shape, and relative thermal resistance to mixing) differed between the regions as hypothesized in H3, owing mainly to differences in lake morphometric variables. Lakes from the LR had shallower thermoclines but greater vertical temperature variability. Since water transparency was similar in both regions, differences in thermal structure were likely a function of the reduced wind fetch and exposure of LR lakes. On the other hand, differences between regions in the thermal resistance to mixing were more related to variables describing the light environment. Thus, the higher stability (RTR) of LR lakes may be explained by the slightly higher water colour observed in this region and its effect in creating a greater temperature differential between surface and deeper water column layers (Dillon *et al.*, 2003; Snucins and Gunn, 2000).

The depth of the peak in bulk phytoplankton was similar in both regions (contrary to our prediction in H4) and defined by temperature and light environment variables. Differences in driving factors of peak depth between the regions were found only for the influence of thermocline depth, which had a more positive influence in the LR. For the spectral groups, only the GREENs had statistically deeper maxima in the ETR. Why this group should differ between regions is unclear since the main factor driving spectral group peak depths in the RDA (water colour measured as absorption at 440 nm) was the least related to the GREENs. It may be because the chlorophytes form a very heterogeneous group in terms of motility, shape and size, they can form unicellular flagellated or non-flagellated cells, colonies or filaments (Lee, 1999). Thus, differences in the positions of the biomass maximum between the regions could have been a result of taxonomic differences and the associated variation in morphological traits within the GREENs which may have allowed for different strategies to dominate in each region. Further taxonomic investigation is required.

A more peaked bulk phytoplankton distribution was observed in the LR (as predicted in H4), where there was a more heterogeneous temperature distribution and a more stable (less mixed) water column. Similarly, heterogeneity in the vertical distribution of the four spectral groups was always higher in the LR, although significant differences between regions were evident only for the BROWNs. For variation in this spectral group, the RDA showed that water colour (A_{440}) was the most important factor. Thus, the more variable

distributions observed for BROWNs in the LR likely resulted from the higher water colour values observed in this region. Taken together, these results on the variation in phytoplankton distribution provide further support for the prediction that a heterogeneous distribution should be associated with strong environmental vertical gradients, under poorly mixed conditions (Klausmeier and Litchman, 2001). As the model of Klausmeier and Litchman (2001) suggests, the important gradients are likely to be the opposing ones of increasing nutrients and decreasing light with depth, common under stratified conditions and likely to have been more pronounced in the LR.

1.5 Conclusions

Our study demonstrates that across many lakes, varying in environmental conditions and morphometry, pronounced temperature gradients favour the distribution of bulk phytoplankton into more defined layers, while the depth of the peak and the heterogeneity of individual phytoplankton groups were differentially affected by habitat structure. Phytoplankton habitat structure was relatively different between the two contrasted regions. Overall, lakes from the LR had shallower thermoclines, higher temperature variability and a greater relative thermal resistance to mixing than lakes from the ETR, owing to differences in wind fetch and exposure, as well as in light climate. Differences in habitat structure between the regions were reflected in differences in the heterogeneity of phytoplankton distribution with a more peaked distribution of bulk phytoplankton and of the four spectral groups in the LR. The depth of the peak in total phytoplankton biomass and for the major phytoplankton groups was similar in both regions, except for deeper maximum of the GREENs in the ETR, which suggests that there may be important differences in the taxonomic composition of this group between regions. Patterns in species composition remain to be explored.

CHAPITRE II

PATTERNS IN TAXONOMIC AND FUNCTIONAL DIVERSITY OF LAKE PHYTOPLANKTON

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Longhi, Maria Lorena and Beisner, Beatrix E.

L'auteure principale de cet article, Maria Lorena Longhi, était responsable et a réalisé : l'échantillonnage de terrain, les analyses de laboratoire, les analyses de données, la recherche bibliographique et la rédaction de l'article. La co-auteure, Beatrix E. Beisner, en qualité de directrice de thèse de Maria Lorena Longhi, était responsable d'orienter et d'apporter ses commentaires dans toute la démarche ayant mené à cet article.

Patterns in phytoplankton diversity in lakes and their relationships with environmental gradients have been traditionally based on taxonomic analyses and indices, even though measures of functional diversity (FD) might be expected to be more responsive to such gradients. We assessed the influence of water column physical structure, and other components of the overall environment, on lake phytoplankton diversity using two taxonomically based indices [species richness (*S*) and the Shannon index (*H'*)] and a FD index, to determine whether these different measures respond in similar ways to habitat structure. The study encompassed 45 lakes in Eastern Canada, within two lake districts [the Eastern Townships Region (ETR) and Laurentians Region (LR)] that vary in geology and landscape and in lake morphometry and chemistry. Across all lakes, *S* and *H'* were higher in lakes having greater vertical temperature heterogeneity and higher susceptibility to wind mixing. In addition, *H'* declined with total phosphorus concentration. FD was only related to maximum lake depth, a variable that integrates many other habitat features. Further insight into the factors affecting phytoplankton diversity was obtained by contrasting the two regions. The taxonomically based diversity measures differed little between the regions, while FD was higher in the ETR where more trait variants were present and more evenly distributed amongst species. Whereas factors driving *S* did not differ between the regions, we found region-dependent patterns in the relationships of *H'* and FD with maximum lake depth: both indices decreased with maximum depth in the region with lakes more exposed to wind (ETR) but increased in the more hilly landscape where lakes are more sheltered from wind mixing (LR). Our study demonstrates that, for phytoplankton communities, a FD index can show simpler and stronger responses to environmental drivers than a taxonomically based index, while shedding further light onto the functional traits that are important in particular lake categories.

2.1 Introduction

Several general diversity patterns have been identified for plankton from freshwater and marine environments (Dodson, Arnott and Cottingham, 2000; Irigoien, Huisman and Harris, 2004; Smith *et al.*, 2005). For example, as observed for many other organisms, Smith *et al.* (2005) found a strong species-area relationship for phytoplankton in both natural and experimental ecosystems. Phytoplankton also show diversity peaks at intermediate levels of productivity (Dodson, Arnott and Cottingham, 2000; Irigoien, Huisman and Harris, 2004). Responses of species diversity to environmental gradients may vary with spatial scale (Chase and Leibold, 2002; Smith *et al.*, 2005), and several explanations have been invoked, including spatial niche differentiation, competition for multiple resources (e.g. light and

nutrients), periodic disturbances, food web structure and colonisation processes (Morin and Fox, 2004; Smith *et al.*, 2005).

A variety of microhabitats are available to phytoplankton during the period of thermal stratification in temperate freshwater lakes. These microhabitats arise because of strong vertical gradients in major environmental factors: temperature, light and nutrients. These factors interact to generate, at least in part, a vertical spectrum of niches, each offering unique conditions to which species are differentially adapted (Clegg, Maberly and Jones, 2007; Reynolds, 1984). It is thought that the simultaneous presence of these niches in a water column contributes to the maintenance of greater diversity (Jäger, Diehl and Schmidt, 2008; Stomp *et al.*, 2007). However, in addition to the presence of a heterogeneous habitat, coexistence requires trade-offs in the responses (acquisition and use) of different species to alternative resource densities (Tilman, 1982). Thus, the differentiation of niches implies a functional complementarity of coexisting species (Loreau, 2004).

The vertical temperature characteristics of a lake, along with other key features like water colour and total nutrient loading, should partly define the niches available to the species and functional groups of phytoplankton. Temperature profiles in high summer largely reflect the penetration of light, especially in clear and/or small stained lakes, since generally (the exception being large, stained lakes; Jones, 1992), for water of a given colour, thermocline depth is related to the heat incorporated in the photic zone (Fee *et al.*, 1996; Jones, 1992; Snucins and Gunn, 2000). Temperature profiles in lakes also largely determine nutrient distributions, as they create a physical barrier to water mixing. Above the thermocline, bioavailable nutrients are generally limiting and below it nutrients are more available owing to decomposition (Fee, 1979) or release from sediments because of anoxic conditions.

Periodic disturbances can also structure phytoplankton communities, and such perturbations may interact with the availability of vertical niches to affect diversity. An intermediate frequency of disturbance is sufficiently stable to allow the formation of assemblages of phytoplankton species, but variable enough to prevent competitive exclusion (Reynolds, 1993; Reynolds, Padisák and Sommer, 1993; Richerson, Armstrong and Goldman, 1970). As a result, no single species dominates strongly and, consequently, more

species can coexist (Reynolds, 1993; Reynolds, Padisák and Sommer, 1993). Furthermore, well-mixed environments have reduced spatial heterogeneity, with algae more homogenously distributed in the water column. In these mixed systems, niche differentiation is consequently reduced and is accompanied by lower diversity (Jäger, Diehl and Schmidt, 2008).

To date, patterns of phytoplankton diversity in lakes and their relationships with environmental gradients have been based mostly on taxonomic analyses (Dodson, Arnott and Cottingham, 2000; Interlandi and Kilham, 2001; Smith *et al.*, 2005). However, measures of functional diversity (FD) might be expected to be more responsive to different spatial resource gradients than traditional taxonomic indices. Early work by Margalef attempted to predict the occurrence of functional groups of marine phytoplankton along gradients of nutrients and turbulence (Margalef, 1978). More recently, studies by Reynolds and collaborators used phytoplankton functional associations, where species were intuitively grouped by similar morphological, physiological and ecological features, and related to different sets of environmental conditions (Kruk *et al.*, 2002; Reynolds *et al.*, 2002). These functional associations were more responsive to environmental factors than taxonomic-based classification (Kruk *et al.*, 2002). Although a broad distribution of common species of phytoplankton can be found in lakes, under certain conditions, particular groups dominate (Reynolds, 1998). Functional traits in phytoplankton include morphological and physiological characteristics that affect essential functional processes including growth, reproduction and nutrient uptake (Weithoff, 2003). The suite of functional characteristics observed in a community can define the complementarity of resource use and may consequently influence ecosystem functions such as primary production and respiration (Loreau *et al.*, 2001; Hooper *et al.*, 2005).

Several methods have been proposed to measure FD in communities (Mason *et al.*, 2005; Petchey and Gaston, 2002; Walker, Kinzing and Langridge, 1999). One common method uses a dendogram approach developed from a matrix of functional traits by species to measure FD (Petchey and Gaston, 2002). FD has been used in a wide variety of taxa (Blackburn *et al.*, 2005; Mouillot, Dumay and Tomasini, 2007; Petchey *et al.*, 2007), including zooplankton (Barnett and Beisner, 2007), but to our knowledge this is its first use for phytoplankton communities.

The overall goal of this study was to assess patterns in taxonomic and FD in phytoplankton communities with respect to lake environmental factors that broadly define the presence and persistence of vertical habitat niches. Our study examined lakes in Southern Québec, Canada, which varied across a wide gradient of environmental productivity, colour and morphometry, to provide a variety of cross-lake niche types as well as variability in within-lake vertical structure. Temperature profiles allowed us to more narrowly define vertical niche partitioning and temporal stability based on the fact that light availability (through sensible heat flux) affects the depth of the epilimnetic zone in lakes (Fee *et al.*, 1996; Snucins and Gunn, 2000), and the fact that the thermocline delimits zones with less (epilimnion) and more (hypolimnion) bioavailable nutrient resources (Fee, 1979). Thus, temperature profiles reflect well, the degree to which light and nutrients vary down the water column and provide an index of phytoplankton niche heterogeneity. We hypothesised (H1) that higher taxonomic and FD of phytoplankton would be found in more spatially heterogeneous habitats (i.e. lakes with greater vertical temperature variation) and particularly in lakes susceptible to some wind mixing (i.e. lakes that simultaneously showed a lower thermal resistance to mixing), a feature that would prevent competitive exclusion that might occur in each niche under completely undisturbed conditions. We further hypothesised (H2) that the relationships would be stronger (more significant with higher R^2) with functional than with taxonomic diversity.

Furthermore, to ensure that patterns observed were robust across lake districts of different types, lakes in two neighbouring areas of Southern Québec were compared. The Eastern Townships Region (ETR) and the Laurentians Region (LR) differ in their geology and surrounding landscape (Pinel-Alloul, Bourbonnais and Dutilleul, 1996; Prairie, Bird and Cole, 2002), as well as in the nature of their coloured dissolved organic carbon (DOC), with a much higher contribution of DOC to the light extinction coefficient in the Laurentians than in the ETR (Prairie, Bird and Cole, 2002). Furthermore, lakes from the former generally have a lower fetch, are more sheltered from wind (Pinel-Alloul, Bourbonnais and Dutilleul, 1996; Prairie, Bird and Cole, 2002) and consequently have shallower thermoclines and greater vertical temperature variability (chap. 1). We further hypothesised (H3), therefore, that phytoplankton diversity patterns would differ between the regions and (H4) that differences in the phytoplankton diversity relationships would be attributable to regional differences in

physical and chemical environments and in morphometric variables, possibly demonstrating higher diversity in the LR where greater temperature variability is present.

2.2 Methods

2.2.1 Study sites and sampling

This study included 45 lakes from the ETR (25 lakes) and the LR (20 lakes). Means and ranges of limnological characteristics for all sampled lakes and for lakes in each region are listed in Table 2.1. Lakes from the ETR are in a well-buffered calcareous region underlain by a sedimentary geology, whereas LR lakes are on the southern part of the Canadian Shield, being underlain by a gneiss-granitic bedrock covered by morainic soils. Sampling was carried out at the deepest point once in each lake in July 2004 for 15 lakes in the ETR and in July 2005 for the other 30 lakes. Our sampling regime attempts to reflect the phytoplankton communities at the point of high summer stratification. However, because we did not sample through time, we cannot say to what degree our measures reflect the communities throughout the entire summer stratification period. To ensure that there was no effect of sampling year on the phytoplankton diversity variables, we performed analyses of covariance (ANCOVAS, see Statistical analyses section) with years as covariate (not shown as this was never a significant covariate).

2.2.2 Physical structure of the water column

Four descriptors characterised the physical structure of the water column in each lake: water transparency, thermocline depth, coefficient of variation of the temperature (CV temp.) profile and mean relative thermal resistance (RTR) to mixing. Water transparency was measured with a Secchi disc (Secchi depth: Z_{Secchi}). Temperature profiles were recorded with a temperature sensor attached to a submersible spectrofluorometer (FluoroProbe; bbe-Moldaenke, Kiel, Germany) (accuracy: 0.1°C). For each lake, thermocline depth (Z_{thermo}) was defined as the depth at which the vertical temperature gradient was the greatest. With the exception of lakes Drolet, St. Georges and Waterloo in the ETR, and Renaud and Walfred in the LR, all water bodies were stratified. For the unstratified lakes, overall lake depth was

Table 2.1
Limnological characteristics across all 45 lakes (ALL), lakes from the Eastern Townships and Laurentians regions

Variable	All lakes			Eastern Townships			Laurentians		
	Min.[a]	Mean	Max.[b]	Min.[a]	Mean	Max.[b]	Min.[a]	Mean	Max.[b]
Maximum depth (m)	4.20	21.65	84.80	4.30	24.37	84.80	4.20	18.26	59.00
Area (km^2)	0.09	2.44	18.71	0.20	3.47	18.71	0.09	1.15	5.31
Fetch (km)	0.33	1.90	7.49	0.39	2.50	7.50	0.33	1.16	2.46
Wind speed (km h^{-1})	6	10	15	6	7	9	13	14	15
Total phosphorus (µg L^{-1})	5.22	17.26	47.98	5.22	15.95	43.78	5.40	18.99	47.98
Dissolved organic carbon (mg L^{-1})	2.07	5.63	9.29	2.27	5.54	8.83	2.07	5.75	9.29
Absorption at 440 nm (m^{-1})	0.00	1.46	3.92	0.00	1.35	3.34	0.00	1.61	3.92
Mean chlorophyll *a* (µg L^{-1})	0.37	2.98	15.34	0.37	3.44	15.34	0.43	2.41	7.86
Secchi depth (m)	1.25	3.97	9.50	1.25	4.07	9.50	1.50	3.85	8.5
Thermocline depth (m)	1.60	5.24	12.40	1.60	6.16	12.40	2.04	4.18	7.6
Coefficient of variation of the temperature	0.00	0.29	0.61	0.01	0.23	0.58	0.00	0.36	0.61
Relative thermal resistance to mixing	0.94	3.36	7.87	0.94	2.36	4.41	1.58	4.61	7.87
Species richness	9	15	22	9	16	22	9	14	21
Shannon index	1.36	2.25	2.96	1.36	2.31	2.96	1.56	2.18	2.73
Functional diversity	0.40	0.57	0.76	0.48	0.59	0.76	0.40	0.54	0.70

[a]Minimum value.
[b]Maximum value.

used to estimate Z_{thermo}. The CV temp. was calculated as the standard deviation of the temperature profile divided by the mean over the photic zone. A higher value of CV temp. indicates a more heterogeneous temperature distribution. Photic zone depth was estimated as $2.79*Z_{Secchi}$ in each lake (Margalef, 1983).

Mean RTR to mixing was used to characterise the stability of the water column at the time of sampling. It was calculated over the photic zone as the average of density differences of all adjacent 10-cm layers relative to the density difference between water at 4 and 5°C according to the formula:

$$RTR = \overline{(\rho 2 - \rho 1) . 10^6 / 8},$$

where ρ_2 and ρ_1 are the densities (g cm^{-3}) at the bottom and the top, respectively, of the stratum being considered and RTR is measured in relative units (Birge, 1910).

2.2.3 Wind speed

For each lake, the nearest weather station with a continuous wind record during the sampling period was used (data from Environment Canada; http://www.climate.weatheroffice.ec.gc.ca/). Reported 24 h-speeds were averaged for the 7 days prior to each sampling event.

2.2.4 Chemical measurements

Water samples for chemical analyses were collected at 0.5 m depth with a 2 L van Dorn bottle. In the laboratory, total nitrogen (TN) and total phosphorus (TP) were measured after alkaline persulphate digestion using an Alpkem autoanalyser (OI Analytical, College Station, TX, U.S.A.) and Ultrospec 2100 pro spectrophotometer (Biochrom, Cambridge, U.K.), respectively. DOC concentrations of filtered water samples (surfactant-free membrane filters) were measured after acidification (sulphuric acid 5%) followed by sodium persulphate oxidation on a 1010 TOC analyzer (OI Analytical). The absorption coefficient at 440 nm (A_{440}), used as a measure of water colour, was measured on filtered (Whatman GF/F) water samples using a 2-cm quartz cuvette (Cuthbert and del Giorgio, 1992) as:

$$A_{440} = 2.303 \cdot (\text{absorbance at } 440 \text{ nm} / 0.02 \text{ m}).$$

2.2.5 Phytoplankton diversity

Phytoplankton was sampled using an integrated sample over the photic zone collected with a flexible PVC tube sampler. Aliquot (250 mL) subsamples were preserved with Lugol's solution. They were later identified to species (when possible) or to genus level and counted using the Utermohl method on an Olympus (model IX 71; Markham, ON, Canada) inverted microscope. Samples were counted at 640X magnification until no new species were encountered during five fields and scanned at 200X magnification through one transect. Approximately, 20 cells of each species (≤5 cells in rare species) were measured in each sample and then converted to biovolume using appropriate geometrical forms (Hillebrand *et al.*, 1999).

Taxonomic phytoplankton diversity was calculated as species richness and the Shannon index. Species richness (S) was measured as the total number of phytoplankton species in each lake community. However, because unequal numbers of cells were counted in the studied lakes, a rarefaction correction (FastGroupII online calculator, http://biome.sdsu.edu/fastgroup/calculation.htm) was applied to standardise and compare species richness from samples of different sizes (Hurlbert, 1971; Sanders, 1968). The Shannon index (H'), which takes in account both the richness and evenness of the species present in each sample, was measured as:

$$H' = - \sum p_i \ln p_i$$

where p_i is the relative biomass of species i and is calculated as the biovolume of a given species i to the biovolume of the entire algal community (Krebs, 1998). The evenness (J') in each lake was measure as:

$$J' = H' / H'_{max}$$

where H'_{max} is the maximum value of H', equal to:

$$H'_{max} = \ln S.$$

To measure FD of phytoplankton, we considered seven functional traits: (i) capacity for nitrogen fixation, (ii) silica demand, (iii) capacity for mixotrophy, (iv) tendency to form chains or colonies, (v) cell motility, (vi) pigment composition and (vii) cell size. Traits were chosen, because they are strongly correlated with ecologically relevant attributes of

phytoplankton such as growth, sedimentation and grazing loss and are all easily measurable or obtainable from the literature (Weithoff, 2003). These traits relate to resource (i.e. nutrients, light) acquisition (traits 1-7), predator avoidance (traits 4-5, 7) and reproduction (trait 7) (Litchman and Klausmeier, 2008). The capacity for nitrogen fixation is a trait that enables acquisition of atmospheric nitrogen (e.g. some cyanobacteria) and provides a competitive advantage under nitrogen-limited conditions (Herrero and Flores, 2008). This was a binary variable in the trait matrix. The silica demand trait (also binary) was included, because diatoms and some silicoflagellates need silica to build their frustules and scales (Lee, 1999). Silica also influences functioning of the community as it increases the plankton's specific weight, especially in diatoms, leading to higher sedimentation rates (Reynolds, 1984). The mixotrophy (binary) trait is related to the ability to feed in both heterotrophic and autotrophic modes (Raven, 1997) and confers an advantage under nutrient-poor conditions (Bird and Kalff, 1987; Laybourn-Parry, Marshall and Marchant, 2005). The trait of tendency to form chains or colonies is particularly relevant for phytoplankton, as it determines susceptibility to zooplankton grazing and affects nutrient acquisition and cell sinking rates (Grover, 1989). Cell motility (categorical variable) may be an asset in environments exhibiting marked nutrient gradients such as stratified lakes, where motile organisms can migrate towards favourable conditions and form patches as well as counteract sedimentation (Clegg, Maberly and Jones, 2007; Visser *et al.*, 1996). Three motility categories were assigned: non-motile cells, buoyancy regulation through gas vacuoles and flagellated species (three-dimensional motility). Pigment composition is a key trait that characterises phytoplankton ability to capture different parts of the visible light spectrum, as well as different light intensities (Falkowski and Raven, 1997; Stomp *et al.*, 2004). The pigment composition of the peripheral antennae of four main spectral groups was used: green containing chlorophyll *a* (chl *a*), chl *b* and xanthophyll, blue with phycocyanin, brown with chl *a*, chl *c* and xanthophyll (fucoxanthin or peredinin), and mixed with chl *a*, chl *c* and phycoerythrin. Information required for the first six traits was obtained from the literature. The final trait, cell size, is related to growth rate (Banse, 1976; Sommer, 1981), zooplankton edibility (Gliwicz, 1977; Lampert *et al.*, 1986), sinking rate (Ptacnik, Diehl and Berger, 2003) as well as nutrient uptake (Grover, 1989; Smith and Kalff, 1982) and was estimated based on the longest linear dimension (LLD) of the cell. LLD is a continuous trait, and mean values

across all lakes for each species were used based on measurements of about 20 cells per species from each lake (≤5 cells in rare species).

Using the functional traits, a community dendrogram based on Gower distances between each pair of species was estimated for the species found in all the studied lakes. The dendrogram was created using the unweighted pair-group clustering method with arithmetic averages (UPGMA method). The FD of each lake was then calculated as the sum of dendrogram branch lengths of only those species found therein (Petchey and Gaston, 2002, 2006). All FD measures were calculated using R2.20 and code obtained online from O. Petchey's Website (http://owenpetchey.staff.shef.ac.uk/Code/Code/calculatingfd.html). We modified their routine to use the Gower distance instead of the Euclidean distance, as this is more appropriate for our mixed (discrete + continuous) traits (Podani and Schmera, 2006, 2007).

2.2.6 Statistical analyses

Principal component analysis (PCA) using environmental variables allowed us to evaluate similarities between lakes and regions. All variables were centred and standardised prior to ordination. PCA was performed using CANOCO version 4.5 (ter Braak, 1990).

Student's *t*-tests were used to test differences in mean values of *S*, *H'* and FD between the two regions. ANCOVAS with region as covariate (after checking for effects of sampling year) were used to identify and compare factors that accounted for the greatest amount of variation between lakes in phytoplankton diversity variables (*S*, *H'* and FD) from the two regions. Independent variables tested were those related to lake morphometry (i.e. Z_{max} and fetch), chemistry (i.e. TP, TN: TP, A_{440}) and physical habitat structure variables (Z_{Secchi}, Z_{thermo}, CV temp. and RTR). ANCOVAS and *t*-tests were carried out using JMP 8.0 (SAS Institute Inc. 2008, Cary, NC, U.S.A.) at $\alpha = 0.05$ level of significance. Variables with non-normal distributions were log transformed prior to analysis, and prior selection of independent variables was made to exclude those that had correlations of > ±0.75.

2.3 Results

2.3.1 Phytoplankton habitat characterisation

Across all lakes and in the two different regions, vectors from the PCAs had similar sizes showing that variability was approximately equally distributed amongst the environmental variables (Fig. 2.1). The PCA combining all lakes showed little overlap among lakes from the ETR and those from the LR (Fig. 2.1A). In this PCA, lakes in the ETR had greater Z_{max}, fetch and Z_{thermo} than those from the LR, which had greater A_{440}, CV temp. and RTR. Across all lakes, there were inverse relationships of Z_{max} and Z_{Secchi} with A_{440} and TP, such that deeper lakes were clearer and more oligotrophic. There was also a positive relationship of lake fetch with Z_{thermo} but an inverse relationship with lake stability (RTR), suggesting that lakes with large fetches had deeper thermoclines and were less stable.

In the PCA for ETR lakes only; the greatest inter-lake variation resulted from differences in morphometry (Z_{max}), chemistry (TP, TN:TP) and light penetration (A_{440}, Z_{Secchi}) (Fig. 2.1B). In the LR, like the ETR, most variation was because of differences in morphometry (Z_{max}) and one light-defining characteristic (Z_{Secchi}). However, in the LR, thermal characteristics were also important (Z_{thermo}, CV temp. and RTR) (Fig. 2.1C). In the ETR, the relationships between environmental variables that had been observed across all lakes were maintained: lake fetch was positively related to Z_{thermo} and inversely to RTR. In the LR, lake stability was more related to light-determining variables (positive with A_{440} and negative with Z_{secchi}) in addition to other morphometric and physical characteristics (Z_{max}, Z_{thermo} and CV temp.). Thus, the most stable lakes in the LR were shallow with higher water colour and shallow Secchi depths.

2.3.2 Phytoplankton composition

Phytoplankton communities consisted mainly of diatoms (on average 26% of total biomass), chrysophytes (21%), cryptophytes (20%), cyanobacteria (17%) and chlorophytes (11%), with smaller contributions of dinoflagellates (3%) and euglenophytes (2%). The relative biomass contributions of major phytoplankton taxa were similar between regions (Student's *t*-tests for comparison of each phytoplankton group were all non-significant).

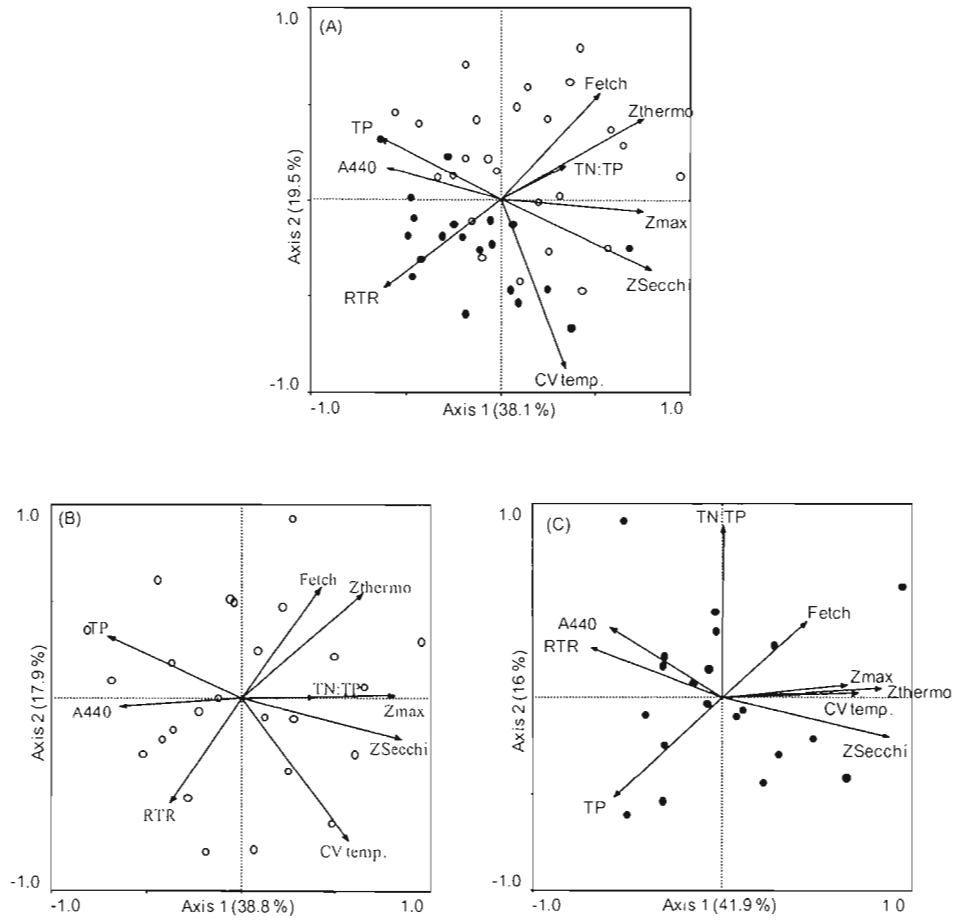


Fig. 2.1. Ordination biplots for the principal component analyses of all environmental variables used in this study [maximum depth (Z_{max}), fetch, total phosphorus (TP), total nitrogen:total phosphorus (TN:TP), absorption at 440 nm (A_{440}), Secchi depth (Z_{Secchi}), thermocline depth (Z_{thermo}), coefficient of variation of the temperature (CV temp.) and relative thermal resistance to mixing (RTR)] (A) for all lakes, (B) for lakes from the Eastern Townships region and (C) for the Laurentians region (LR). Open circles represent lakes from the Eastern Townships and solid circles from the LR. Arrows represent each environmental factor.

2.3.3 Phytoplankton diversity

Across all lakes, species richness (S), after rarefaction, varied from 9 to 22 (Table 2.1, Fig. 2.2A, B). Mean S per lake was slightly higher in the ETR than the LR (Student's t-test: $t = -1.52$, $P = 0.0682$, d.f. = 43). Shannon diversity varied widely across all lakes with an average value of 2.25 (Table 2.1, Fig. 2.2C, D), but mean values did not differ between regions ($t = -1.16$, $P = 0.1261$, d.f. = 43). FD in most lakes ranged between 0.50 and 0.60 (Table 2.1, Fig. 2.2E, F), with a higher mean FD in the ETR ($t = -2.63$, $P = 0.0059$, d.f. = 43). Lakes with the highest FD (>0.65) were all from the ETR (Lakes Baldwin, Fitch, Petit Lac Brompton and Des Monts) with one exception (Lake Achigan in the LR). The lowest value of FD (=0.40) was observed in the LR (Lake Renaud). The next lowest FD values (0.45-0.50) included three lakes from the LR (Lakes Nord, Cromwell and Morency) and two from the ETR (Lakes Bowker and Magog).

2.3.4 Factors affecting phytoplankton diversity

Species richness in all lakes was negatively related to RTR and positively to CV temp. (Table 2.2, Fig. 2.3). No differences in this relationship were observed between the regions (ANCOVA, $P = 0.0048$, $R^2_{adj.} = 0.31$).

Phytoplankton diversity (Shannon index, H') in all lakes combined showed responses to several environmental variables (ANCOVA, $P = 0.0033$, $R^2_{adj.} = 0.31$; Fig. 2.4, Table 2.2). Diversity declined with TP concentration across all lakes (Fig. 2.4A, Table 2.2). There were also effects of lake depth (Z_{max}), CV temp. and RTR on H' with relationships that differed between regions (Table 2.2). H' was negatively related to Z_{max} in the ETR (slope= –0.04) but was positively related in the LR (slope= 0.09) (Fig. 2.4B). The positive relationship between H' and CV temp. was slightly stronger in the ETR than in the LR (ETR slope = 0.04 *vs.* LR slope = 0.02) (Fig. 2.4C). Finally, the relationship between H' and RTR was negative in both regions, but the slope was slightly stronger (although not easily seen in the figure) in the ETR than in the LR (ETR slope = –0.074 *vs.* LR slope = –0.068) (Fig. 2.4D). Coefficients of variation (r^2) were low for the relationships of H' with CV temp. and RTR (Table 2.2) probably because there were, respectively, fewer data points (= sampled lakes) at low CV temp. and a high dispersion of points.

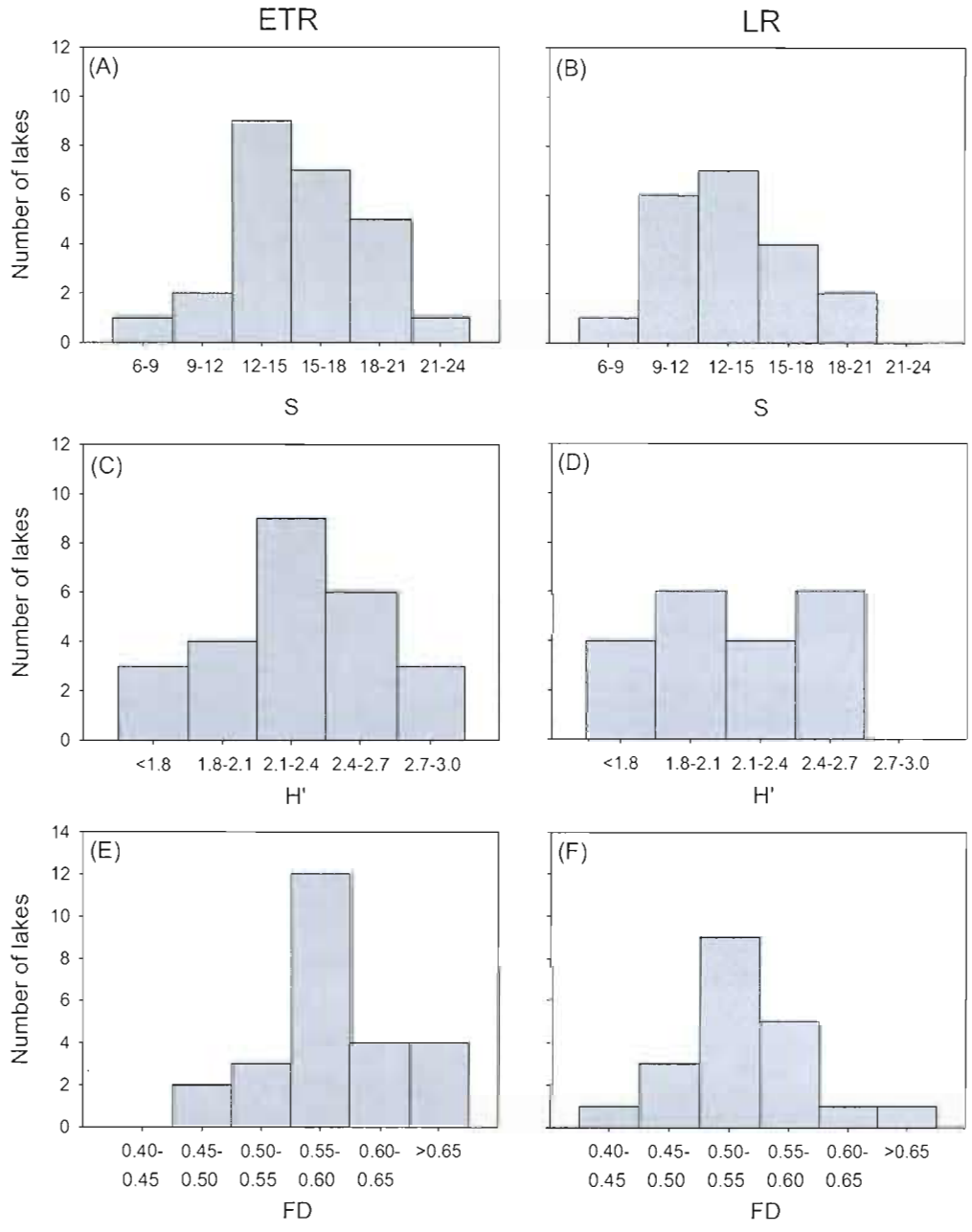


Fig. 2.2. Distributions of phytoplankton species richness after rarefaction (*S*), Shannon index (*H'*) and functional diversity (FD) in the Eastern Townships (A, C, E) and Laurentians (B, D, F) regions.

Table 2.2

Results of ANCOVAs for the three phytoplankton diversity measures testing for overall and regional differences in environmental driving variables

	Coefficient (SE)	P	P_{global}	r^2	$R^2_{adj.}$
Log_{10}Species richness					
Constant	1.3024 (0.0426)	<0.0001	0.0048		0.31
Log_{10}RTR	-0.1756 (0.0602)	0.0057		0.13	
Log_{10}CV temp.	0.0728 (0.0286)	0.0150		0.14	
Log_{10}Shannon index					
Constant	0.4409 (0.0556)	<0.0001	0.0033		0.31
Log_{10}TP	-0.0854 (0.0462)	0.0412		0.10	
$Log_{10}Z_{max}$*region	-0.1804 (0.0460)	0.0372		0.10	
Log_{10}CV temp.*region	0.1040 (0.0327)	0.0357		0.09	
Log_{10}RTR*region	-0.1727 (0.0673)	0.0318		0.09	
Log_{10}Functional diversity					
Constant	-0.2486 (0.0066)	<0.001	0.0004		0.33
Region	0.0190 (0.0066)	0.0062		0.19	
$Log_{10}Z_{max}$*region	-0.0645 (0.0202)	0.0026		0.18	

Independent variables tested included maximum depth (Z_{max}), fetch, total phosphorus (TP), total nitrogen:total phosphorus, absorption at 440 nm, Secchi depth, thermocline depth, coefficient of variation of the temperature (CV temp.) and relative thermal resistance (RTR) to mixing. All variables were log_{10} transformed.

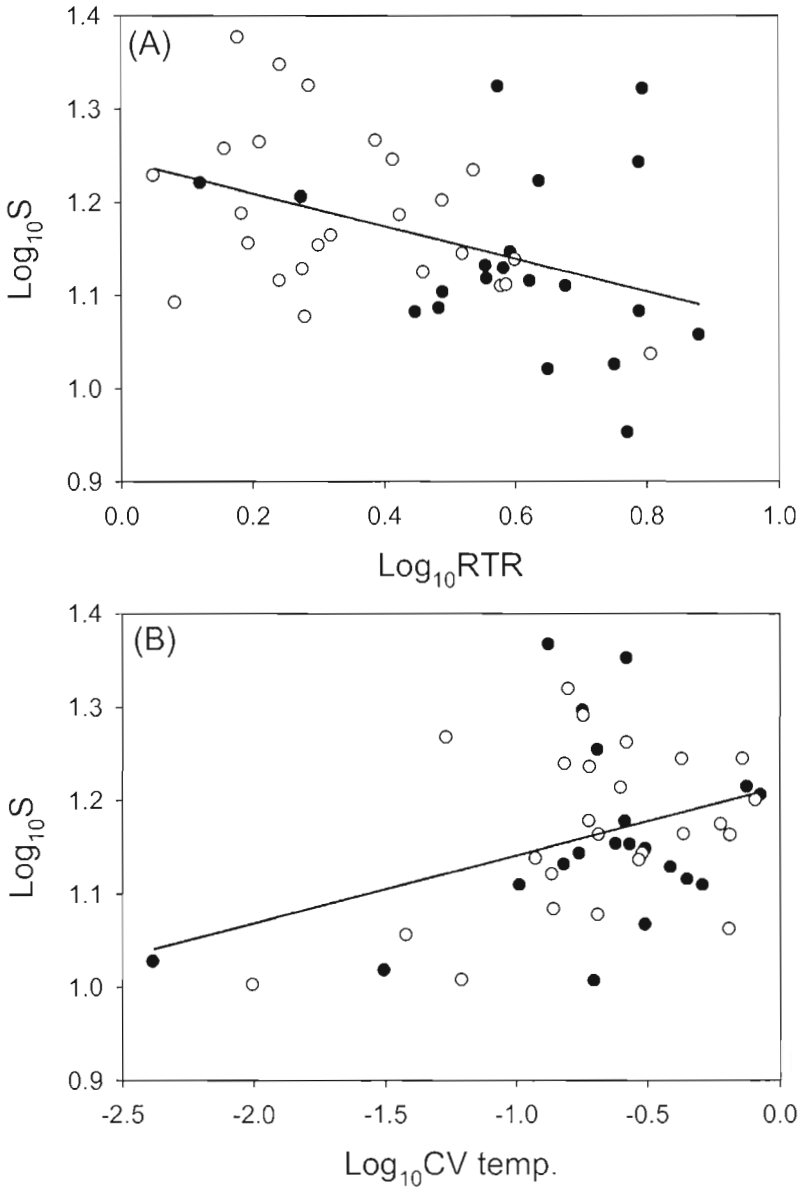


Fig. 2.3. Partial regression plots from a model relating species richness after rarefaction (*S*) to (A) relative thermal resistance (RTR) to mixing and (B) coefficient of variation of the temperature (CV temp.) for lakes from the Eastern Townships (open circles) and Laurentians (solid circles) regions. All variables were $\log_{10}$ transformed.

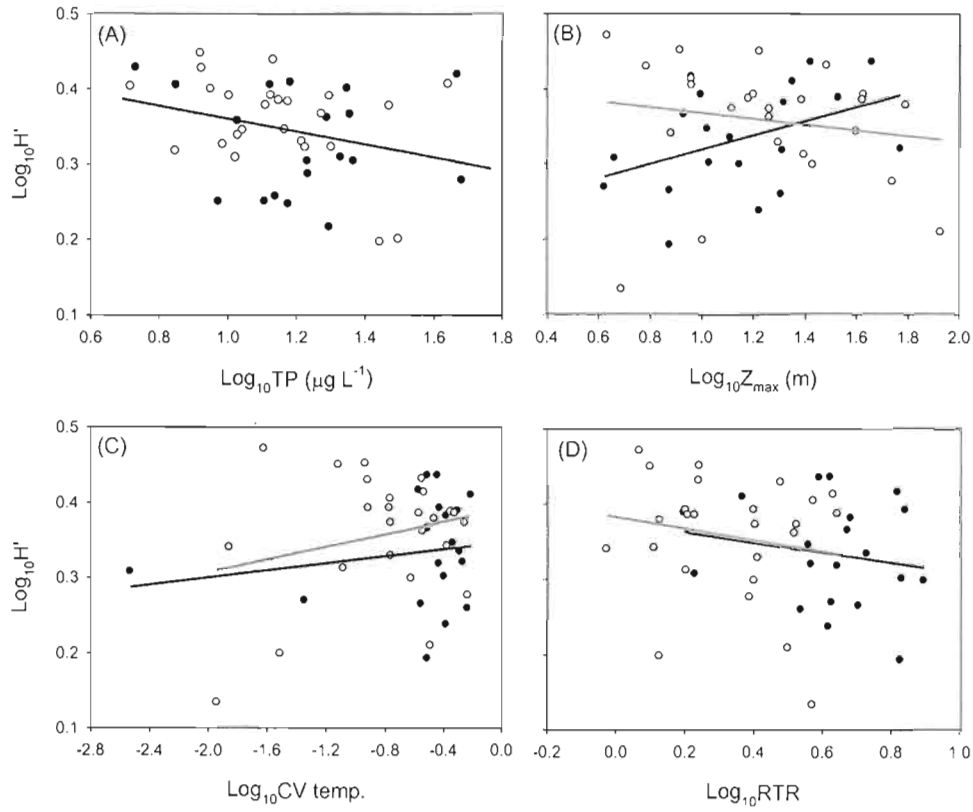


Fig. 2.4. Regression model relating the Shannon index (*H'*) to (A) total phosphorus (TP), (B) maximum lake depth (Z_{max}), (C) coefficient of variation of the temperature (CV temp.) and (D) relative thermal resistance (RTR) to mixing for lakes from the Eastern Townships (open circles) and Laurentians (solid circles) regions. All variables were $\log_{10}$ transformed.

For FD, Z_{max} was the only significant explanatory variable. The ANCOVA revealed that this relationship differed significantly between the regions (P = 0.0004, R^2_{adj} = 0.33, Table 2.2), being negative in the ETR (slope= –0.07) and positive in the LR (slope= 0.06) (Fig. 2.5).

2.4 Discussion

2.4.1 Phytoplankton diversity across all lakes

The results support our first hypothesis (H1) that phytoplankton diversity would be higher in lakes with more heterogeneous habitats and particularly those susceptible to wind mixing. We found that the simplest measure of diversity, species richness, was higher in lakes with greater vertical heterogeneity in temperature as well as with less resistance to wind mixing (lower stability of the water column). In such lakes, we would expect the existence of several habitat layers for phytoplankton in the water column, each with somewhat different characteristics, but that these would be mixed frequently enough to prevent competitive exclusion from occurring in each layer. This form of spatial-temporal heterogeneity thus created a form of 'intermediate-disturbance' (*sensu* Connell, 1978), and in these environments, more species coexist.

Shannon diversity, which reflects both richness and evenness, demonstrated the same overall pattern as S, being greater in thermally heterogeneous habitats that are susceptible to wind mixing, further supporting H1. However, we also observed a negative effect of total phosphorus concentration on H'. TP provides an index of primary production (standing crop) in our lakes, where there is a significant positive correlation between TP and phytoplankton biomass (correlation coefficient = 0.67), as others have found in these regions (Giani *et al.*, 2005; Masson, Pinel-Alloul and Smith, 2000). High TP concentrations have been associated with phytoplankton blooms, accompanied by lower diversity (Leibold, 1999; Scheffer *et al.*, 1997), and this is a possible explanation for our observation of reduced diversity in our eutrophic lakes. A combination of selective grazing and shading is thought to be responsible for lower phytoplankton diversity under bloom conditions (Irigoien, Huisman and Harris, 2004). Based on several lines of evidence and reasoning, however, one might instead expect peak phytoplankton diversity to have occurred at intermediate TP levels (Dodson, Arnott and

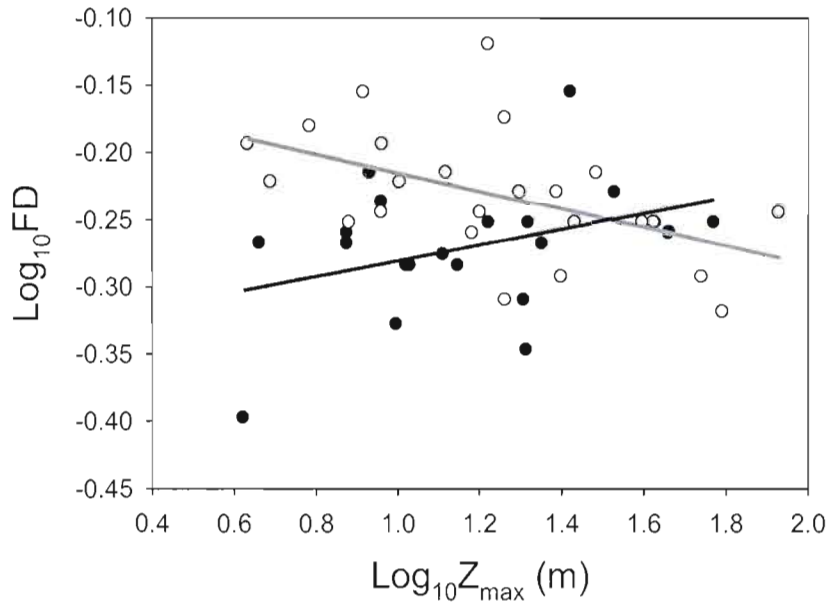


Fig. 2.5. Regression model relating functional diversity (FD) to maximum lake depth (Z_{max}) for lakes from the Eastern Townships (open circles) and Laurentians (solid circles) regions. All variables were $\log_{10}$ transformed.

Cottingham, 2000; Irigoien, Huisman and Harris, 2004). Mechanistically, this is expected to occur when there is competition for multiple resources where superior competitors for nutrients and light dominate at low and high TP, respectively, while a diverse mixture persists at intermediate levels (Morin and Fox, 2004). In addition, we observed a strong biomass dominance (lower H' with less evenness) by cyanobacteria in some of our high TP lakes (e.g. Lakes Waterloo (H' = 1.36, J' = 0.45) and Trois Lacs (H' = 1.58, J' = 0.57). Furthermore, the large cyanobacteria typical of our eutrophic lakes usually escape herbivory by zooplankton (Elser and Goldman, 1991; Gliwicz and Lampert, 1990). Zooplankton diversity (S and FD) also declined with increasing TP from a subset of our study lakes, with eutrophic lakes being mainly dominated by smaller, less competitive herbivorous zooplankton species (Barnett and Beisner, 2007). Oligotrophic lakes, on the other hand, were more likely to contain a diversity (high FD) of zooplankton body sizes and trophic groups feeding mainly on chrysophytes and diatoms (Barnett and Beisner, 2007; Barnett, Finlay and

Beisner, 2007). Such top-down effects along the TP gradient, ranging from a variety of herbivore feeding strategies to very few strategies and body sizes (low FD), may have further accentuated the pattern of decline of phytoplankton diversity (H') with TP.

We set out to examine not just traditional diversity measures but also those that are more related to niche relationships and which may better account for diversity patterns across gradients of habitat type and availability. High values of FD imply a greater number of traits represented and/ or a more equitable distribution of traits among the species in a lake (see Appendix C for some cases). For example, in the lake with the greatest phytoplankton FD (Lake Fitch), all possible nominal traits were present, and the range of cell sizes (continuous trait) was very large (Appendix C). On the other hand, in lakes with the lowest FD, some trait variants were absent or were present in only very few species. Thus, in Lake Renaud, which showed the lowest FD, the traits for nitrogen fixation and motility by buoyancy were absent, and silica demand was rare (Appendix C). Moreover, lakes with low FD had narrow cell size ranges. In other types of organisms, the maintenance of more traits and consequently higher FD has been attributed to increasing S, habitat availability (through temporal and spatial heterogeneity) and/or food source variety (Blackburn *et al.*, 2005; Barnett and Beisner, 2007; Mouillot, Dumay and Tomasini, 2007). In our study, increasing the number of phytoplankton species present had a positive but moderate effect on FD (slope: 0.001, $R^2_{adj.} = 0.23$, $P = 0.0005$, not shown). The main relationships found were between FD and maximum lake depth but with opposing patterns in the two regions, the focus of the discussion in the next section.

The most appropriate definition and measure of FD (e.g. the number and choice of traits, the statistical intricacies of the measure used) have been a matter of exhaustive discussion and debate (e.g. Petchey and Gaston, 2006, 2009; Podani and Schmera, 2006, 2007). However, in our study, along the same lake environmental gradients, the simplest and strongest relationship (based on a slightly higher $R^2_{adj.}$, as predicted by H2) among the three diversity indices used was found for FD with Z_{max}. This simple relationship may reflects a clearer response to a variable (Z_{max}) that integrates across many others (i.e. TN:TP, TP, A_{440}, Z_{Secchi}, Z_{thermo}, CV temp. and RTR, as demonstrated in the PCAs). Over these environmental gradients, the number and type of niches available for phytoplankton should change, and the

number of species present in a community (species richness) will be relevant only if additional species are functionally complementary and able to take over unoccupied niches (Walker, Kinzing and Langridge, 1999). Taking the role of diversity one step further, studies that have focused on the relationship between biodiversity and ecosystem functioning (e.g. productivity, respiration, etc.) have demonstrated that it is the functional characteristics or attributes of species that are important, and not simply the number of species present in a community (see Hooper *et al.*, 2005 and references therein).

2.4.2 Contrasting lake districts

The main difference between lake districts in the diversity patterns was opposing relationships between Shannon diversity and maximum lake depth: H' decreased very slightly with Z_{max} in the ETR, while it increased to a larger degree in the LR. This despite the fact that mean H' was similar in the two regions (but with a wider range in the ETR). Meanwhile, species richness showed little distinction between the regions, and the relationships between S with temperature heterogeneity and the relative resistance of the water column to wind mixing were similar in both regions. The explanation behind the different regional patterns in Shannon diversity is probably similar to those for FD which showed a similar contrasting pattern.

Contrary to expectation (H4), mean FD was higher in the ETR than in the LR. Thus, more variants in traits such as nitrogen fixation, silica demand, pigment composition and cell size were more frequently and equally distributed among species from the ETR lakes. Study lakes from the ETR were more variable in terms of size (depth and surface area), macrophyte cover and zooplankton composition (chap. 1; R. Vogt, personal communication). Thus, lakes from this region could show a greater availability of habitats and more potential herbivores that could explain higher mean FD values for phytoplankton. As for the Shannon index, FD decreased with maximum lake depth in the ETR but increased in the LR.

Overall, lake depth, which reflects differentiation and stability of phytoplankton habitat appears to be the primary factor leading to differences between the two regions. Despite the fact wind speed in mid-summer was higher in the LR than in the ETR, shallow lakes from the LR had lower temperature variation and were very stably stratified (high RTR, as observed

from the PCA for the LR), probably because most small lakes in this region are well sheltered from wind. Consequently, we would expect fewer stable thermal habitats for phytoplankton because of lower spatial temperature variation but also because of lower availability of temporal habitats, since the water columns are less often subject to periodic mixing. It is in these shallow LR lakes that we observed lowest H' and FD, owing to a greater dominance by a few species (4–6 species represented *c.* 75-80% of total biomass) and low trait variance (Appendix C). Cryptophytes, chrysophytes and some dinoflagellate species dominated the biomass in most of these lakes. The traits of nitrogen fixation, silica demand and motility by buoyancy regulation were absent or rare (present in <20% of species), and the size range of the phytoplankton cells was very narrow (Appendix C). These shallow stable lakes, with low vertical temperature heterogeneity, would have had fewer potential phytoplankton niches, and consequently, we observed a lower diversity, further supporting H1. Lakes in the ETR, on the other hand, were more exposed to wind than their counterparts from the LR because of larger fetches and a less forested and hilly landscape. Shallow lakes in the ETR showed a higher taxonomic (H') and FD than deeper lakes in the ETR and shallow ones in the LR. In these lakes, phytoplankton biomass was dominated by a larger number of species (9–11 species represented about 75% of total biomass), all nominal trait variants were present and were more equally distributed among species (with the exception of Des Monts where nitrogen fixation and buoyancy traits were absent), and cell size showed a wider range. Periodic wind mixing in the shallow ETR lakes could resuspend benthic or sedimented microalgae as well as algal cysts and littoral periphyton, phenomena that can increase not only the number and evenness of species (H' was slightly negatively related to maximum lake depth) but also the number of functional traits represented in the planktonic community (for which stronger patterns were observed). Furthermore, the lower TN: TP ratio of these shallow ETR lakes would favour the occurrence of species that have the capacity to fix atmospheric nitrogen, as is the case for some cyanobacteria (Herrero and Flores, 2008), further increasing the number of traits observed in these lakes.

CHAPITRE III

SEASONAL AND LANDSCAPE VARIATION IN VERTICAL DISTRIBUTION AND DIVERSITY PATTERNS OF LAKE PHYTOPLANKTON

Article qui sera soumis dans un journal scientifique.
Longhi, Maria Lorena and Beisner, Beatrix E.

L'auteure principale de cet article, Maria Lorena Longhi, était responsable et a réalisé : l'échantillonnage de terrain, les analyses de laboratoire, les analyses de données, la recherche bibliographique et la rédaction de l'article. La co-auteure, Beatrix E. Beisner, en qualité de directrice de thèse de Maria Lorena Longhi, était responsable d'orienter et d'apporter ses commentaires dans toute la démarche ayant mené à cet article.

Temporal variation in summer stratification modifies the vertical availability of nutrients and the light with consequences for phytoplankton. We examined patterns in composition, distribution and diversity in phytoplankton communities with respect to lake environmental factors across 18 lakes of eastern Canada at three distinct time periods: late spring, mid-summer and early autumn. In most lakes, changes in community composition through the growing season followed the succession pattern expected for dimictic temperate lakes with the exception of shallow, most eutrophic lakes, which were always dominated by cyanobacteria or chlorophytes. Measures of vertical biomass distribution included the depth of peak biomass and the coefficient of variation (CV) of bulk and spectral group biomass. The depth of peak biomass was related to lake depth and wind fetch but with variation through the season. Furthermore, in eutrophic lakes where there was little to no stratification peak biomass was shallower. Throughout the growing season, pronounced temperature gradients favoured the distribution of bulk phytoplankton into more defined layers. For the individual spectral groups of phytoplankton, the vertical location of the peaks did not vary through time. Peak depths of groups, were mainly related to water colour and transparency, with idiosyncratic group responses. Vertical variation in spectral group biomass was most homogeneous in the autumn with no obvious driving factor, but was mainly related to lake morphometry and thermal structure in the spring and summer. Highest diversity was observed in mid-summer and at this time, richness and functional diversity (FD) were greatest in shallow lakes. FD was higher in lakes with darker waters in all periods and with greater zooplankton biomass in spring and autumn. Vertical temperature variation showed only a minor relationship with one diversity measure (Shannon) throughout the study.

3.1 Introduction

Habitat heterogeneity in lakes plays a key role in controlling the abundance, distribution and diversity of phytoplankton (Clegg, Maberly and Jones, 2007; Klausmeier and Litchman, 2001; Reynolds, 1984). Heterogeneity in the water column is represented mainly by vertical gradients in temperature, light and often nutrients. In North Temperate lakes, the summer thermocline is a predominant physical factor that is likely to affect phytoplankton community composition because it restricts the availability of both nutrients and gases and can prevent less motile phytoplankton from sinking into the aphotic zone (Fee, 1976; Reynolds, 1984). Temperature profiles in high summer may also reflect the penetration of light, especially in clear and/or small stained lakes, because for a given water colour, thermocline depth is related to the heat incorporated in the photic zone (Fee *et al.*, 1996; Jones, 1992; Snucins and Gunn, 2000). Variation in environmental conditions across depth

defines the niches [*sensu* Grinnell (Grinnell, 1917)] available to various phytoplankton species and functional groups (Clegg, Maberly and Jones, 2007; Reynolds, 1984). Therefore, strong environmental gradients in the water column should favour the distribution of phytoplankton into defined layers and lead to increases in diversity (Clegg, Maberly and Jones, 2007; Klausmeier and Litchman, 2001; Reynolds, 1984).

Temporal variation in the shape of the summer thermocline (e.g.: during its formation in spring and destruction in fall) modifies the vertical distribution of nutrients and the light climate (Reynolds, 1989, 1990; Sommer *et al.*, 1986) and consequently, the distribution and composition of the phytoplankton could also change (Berger *et al.*, 2007; Sommer *et al.*, 1986) as captured by the 'Plankton Ecology Group' (PEG) model (Sommer *et al.*, 1986). To summarize, with the onset of stratification in spring, mixing depth is reduced, resulting, especially in deep lakes, in an increase in the time algae spend in the euphotic zone. Fast growing flagellates, such as cryptophytes and small centric diatoms should dominate in spring, thereby allowing the phytoplankton community biomass to increase to a distinct spring maximum (Sommer *et al.*, 1986). The spring bloom is generally followed by a clear water-phase, a period with low phytoplankton biomass. This decline in edible algae, during the time when stratification becomes most accentuated and stable, can be attributed to both a reduction of nutrient-rich upwelling to the epilimnion and intense grazing by large herbivorous zooplankton resulting from the earlier phytoplankton peak (Huppert, Blasius and Stone, 2002; Lampert *et al.*, 1986; Sarnelle, 1993; Sommer *et al.*, 1986). When zooplankton population sizes and hence, grazing pressure, are later reduced (mid-summer), and as non-limiting concentrations of nutrients are reestablished, the phytoplankton biomass is expected to increase. At this time, phytoplankton species richness should increase and become more functionally-diversified with representation by both small (e.g.: cryptophytes) and large species (e.g.: colonial green algae) (Sommer *et al.*, 1986). As summer progresses, green algae are replaced by a succession of large diatoms, then by dinoflagellates and/or cyanobacteria. Toward the end of summer or in early autumn, an increase in mixing depth during destratification is expected to result in epilimnetic nutrient enrichment and a deterioration of the effective underwater light climate. Phytoplankton communities should become dominated by functional types that are well adapted to mixed conditions, such large unicellular or

filamentous forms. These less edible phytoplankton may be commonly associated with a variable biomass of small, edible algae (Sommer *et al.*, 1986).

The overall goal of this study was to assess patterns in distribution, composition and diversity in phytoplankton communities through a seasonal succession across a landscape of lakes. We examined 18 lakes in Southern Québec, Canada at three distinct time periods: late spring, mid-summer and in the early autumn. Our lakes varied across a wide gradient of morphometry, environmental productivity and colour. Because seasonal changes in temperature profiles are associated with changes in light climate and nutrient availability in the water column as well as with the density properties of water, we hypothesized (H1) that the vertical distribution of phytoplankton biomass (e.g. depth of maximum biomass and coefficient of variation) would vary across the season. Specifically, we expected deeper peaks of phytoplankton biomass in spring when light penetration and wind-induced mixing are generally greater. In mid-summer when the thermocline is well established and there is a greater thermal resistance to wind mixing, we expected a higher heterogeneity in phytoplankton distribution. Finally in autumn, light levels are reduced and there is greater mixing again in which case we expect either greater homogeneity in the phytoplankton distribution or shallow water peaks by buoyant species. Based on the specific resource requirements and differential abilities of phytoplankton species to move in the water column, we further hypothesized (H2) that the vertical distribution (e.g. depth of maximum biomass and coefficient of variation) of major phytoplankton groups would respond differently to changes in physical structure across the season. Furthermore, because changes in the physical structure of the water column should be accompanied by a change in the availability of different phytoplankton niches, we hypothesized (H3) that there should be differences through time in the diversity of phytoplankton. We expected higher taxonomic and functional diversity with greater spatial heterogeneity, driven mainly by variation in vertical temperature regimes and thus maximized in mid-summer.

3.2 Methods

3.2.1 Study sites and sampling

We studied 18 lakes from the Eastern Townships Region of Southern Québec. The region is well-buffered by calcareous rock and underlain by a sedimentary geology. Sampling was done at the deepest point in each lake within the first two weeks of June, July and September 2004, corresponding to late spring, mid-summer and early autumn thermal stratification. Limnological characteristics for all lakes (means and ranges) during each month are shown in Table 3.1. In general, deeper lakes were clearer and more oligotrophic, whereas lakes with greater fetch had deeper thermoclines and were also less stable (chap. 2).

3.2.2 Physical structure of the water column

Four descriptors characterized the physical structure of the water column in each lake: water transparency, thermocline depth, coefficient of variation of the temperature profile and mean relative thermal resistance to mixing. Water transparency was measured using a Secchi disc (Secchi depth: Z_{Secchi}). Temperature profiles were recorded with a temperature sensor attached to a submersible spectrofluorometer (FluoroProbe, bbe-Moldaenke, Kiel, Germany) (accuracy: 0.1°C). For each lake in each month, thermocline depth (Z_{thermo}) was defined as the depth at which the vertical temperature gradient was the greatest. For the unstratified lakes, overall lake depth was used as the value for Z_{thermo}. One lake (Tomcod) never stratified. One other lake was unstratified in June (Lake St. Georges) and in July (Lake Waterloo) and three others in September (Lakes Brome, St. Georges and Waterloo). The coefficient of variation of the temperature gradient (CV temp.) was calculated as the standard deviation of the temperature profile divided by the mean over the photic zone. A higher value of CV temp. indicates a more heterogeneous temperature distribution. Photic zone depth was estimated as $2.79*Z_{Secchi}$ in each lake (Margalef, 1983).

Mean relative thermal resistance (RTR) to mixing was used to characterize the stability of the water column at the time of sampling. It was calculated over the photic zone as the average of density differences of all adjacent 10 cm layers relative to the density difference

Table 3.1
Chemical, physical and biological characteristics of all lakes

Variable	June			July			September		
	Min.[a]	Mean	Max.[b]	Min.[a]	Mean	Max.[b]	Min.[a]	Mean	Max.[b]
Maximum depth (m)	1.80	20.88	61.90						
Area (km^2)	0.23	2.89	14.50						
Fetch (km)	0.40	2.38	6.86						
Wind speed ($km\ h^{-1}$)	7	10	15	6	7	9	7	8	10
Epilimnetic total phosphorus ($\mu g\ L^{-1}$)	5.22	19.30	79.35	5.22	21.24	101.96	4.87	25.49	114.00
Absorption at 440 nm (m^{-1})	0.26	1.60	3.60	0.35	1.46	3.34	0.11	1.83	6.62
Mean chlorophyll *a* ($\mu g\ L^{-1}$)	0.70	5.03	36.90	0.99	5.50	21.92	0.92	6.45	33.36
Secchi depth (m)	0.40	3.05	7.50	0.75	3.67	9.50	0.50	3.35	8.50
Thermocline depth (m)	1.80	6.10	14.30	1.60	6.22	12.40	0.85	7.19	13.70
Coefficient of variation of the temperature	0.00	0.11	0.25	0.02	0.16	0.47	0.00	0.11	0.50
Relative thermal resistance to mixing	0.18	1.09	3.97	0.82	1.76	3.75	0.36	1.29	2.02
Depth of maximum chlorophyll *a* (m)	0.40	4.91	15.80	0.10	4.42	12.60	0.50	3.67	14.00
Coefficient of variation of chlorophyll *a*	0.03	0.33	0.78	0.04	0.35	0.96	0.03	0.22	0.58
Species richness	9	15	20	12	17	23	7	14	19
Shannon index	1.07	2.04	2.44	1.80	2.42	2.96	0.82	2.19	2.82
Functional diversity	0.37	0.55	0.72	0.48	0.61	0.76	0.43	0.58	0.74

[a]Minimum value.
[b]Maximum value.

between water at 4° and 5°C according to the formula:

$$RTR = \sqrt{(\rho 2 - \rho 1) . 10^6 / 8},$$

where ρ_2 and ρ_1 are the densities (g cm^{-3}) at the bottom and the top, respectively, of the stratum being considered and RTR is measured in relative units (Birge, 1910).

3.2.3 Wind speed

For each lake, the nearest weather station with a continuous wind record during each sampling period was used (data from Environment Canada; *www.climate.weatheroffice.ec.gc.ca/*). Reported 24h-speeds were averaged for the 7 days prior to each sampling event.

3.2.4 Chemical measurements

Water samples for chemical analyses were collected at 0.5 m depth with a 2 L van Dorn bottle. In the laboratory, total nitrogen (TN) and total phosphorus (TP) were measured after alkaline persulfate digestion using an Alpkem autoanalyser (O.I. Analytical, College Station, TX, USA) and Ultrospec 2100 pro spectrophotometer (Biochrom, Cambridge, UK), respectively. Dissolved organic carbon (DOC) concentrations of filtered water samples (surfactant-free membrane filters) were measured after acidification (sulphuric acid 5%) followed by sodium persulfate oxidation on a 1010 TOC analyzer (O.I. Analytical, College Station, TX, USA). The absorption coefficient at 440 nm (A_{440}), used as a measure of water colour, was measured on filtered (Whatman GF/F) water samples with a 2 cm quartz cuvette (Cuthbert and del Giorgio, 1992) as:

$$A_{440} = 2.303 \cdot (\text{absorbance at } 440 \text{ nm} / 0.02 \text{ m}).$$

3.2.5 Phytoplankton measurements

Vertical profiles of total and major taxonomic group biomass were measured *in situ* using a FluoroProbe. The instrument measures fluorometrically the concentration of chlorophyll *a* (Chl *a*) in µg L^{-1} of four major spectral groups of phytoplankton, representing broadly the taxonomic classes of diatoms + dinoflagellates + chrysophytes (hereafter called

"BROWN"), chlorophytes ("GREEN"), cyanophytes containing phycocyanin ("CYANO"), and cryptophytes ("CRYPTO"). Fluorescence of dissolved organic matter ("yellow substances") was subtracted from original fluorescence measurements by using an UV-B excitation source which allows the differentiation between algal fluorescence and fluorescence of "yellow substances" (Beutler *et al.*, 2002). Biomass measured for each phytoplankton group corresponds well with HPLC analysis (Beutler *et al.*, 2002), with traditional Chl *a* extraction techniques (Gregor and Maršálek, 2004) and with taxonomic analyses (Gregor *et al.*, 2005). In our study, total biomass measured with the FluoroProbe were well correlated with Chl *a* estimated by spectrophotometric measurements (chap. 1). In addition, mean relative biomass of each spectral group calculated from the FluoroProbe correspond well with microscope analyses (chap. 1). FluoroProbe profiles were obtained by starting at the lake surface and taking readings at approximately 1 cm intervals. To avoid variability in the descent speed of the probe at the centimetre scale, we took the average value of every 10 cm interval (there were generally 7 to 10 data points per interval). Mean total phytoplankton biomass and average biomass of the four spectral groups were measured from the FluroProbe profiles over the photic zone. Depth of maximum biomass was defined as the depth at which the biomass was the greatest (total Chl *a* or by spectral group). When no clear single peak was observed (i.e. a relatively homogeneous distribution of biomass), we used the depth at which the shallowest distinctive peak in biomass was observed. Vertical heterogeneity of biomass was estimated as the coefficient of variation (CV) of observed values over the photic zone: lower CV's suggesting a more uniform photic zone distribution.

3.2.6 Phytoplankton diversity

Phytoplankton were sampled using an integrated sample over the photic zone collected with a flexible PVC tube sampler. Aliquot (250 ml) subsamples were preserved with Lugol's solution. They were later identified to species (when possible) or to genus level and counted using the Utermohl method on an Olympus (model IX 71) inverted microscope. Samples were counted at 640X magnification until no new species were encountered in five consecutive fields of view and scanned at 200X magnification through one transect. Approximately 20 cells of each species ($\leq$ 5 cells in rare species) were measured along major

dimensions in each sample and then converted to biovolume using appropriate geometrical forms (Hillebrand *et al.*, 1999).

Taxonomic phytoplankton diversity was calculated as species richness and the Shannon index. Species richness (S) was measured as the total number of phytoplankton species in each lake community. However, because unequal numbers of cells were counted in the studied lakes, a rarefaction correction (FastGroupII online calculator, *http://biome.sdsu.edu/fastgroup/calculation.htm*) was applied to standardize and compare species richness from samples of different sizes (Hurlbert, 1971; Sanders, 1968). The Shannon diversity index (H'), which takes in account both the biomass and evenness of the species present in each sample, was measured as:

$$H' = - \sum p_i \ln p_i$$

where p_i is the relative biomass of species i, and is calculated as the biovolume of a given species i relative to the biovolume of the entire algal community in that lake (Krebs, 1998). The evenness (J') in each lake community was calculated using:

$$J' = H' / H'_{max}$$

where H'_{max} is the maximum value of H', equal to:

$$H'_{max} = \ln S$$

To measure functional diversity (FD) of phytoplankton, we considered seven functional traits: (1) capacity for nitrogen fixation, (2) silica demand, (3) capacity for mixotrophy, (4) tendency to form chains or colonies, (5) cell motility, (6) pigment composition and (7) cell size. Traits were chosen because they are strongly correlated with ecologically relevant attributes of phytoplankton such as growth, sedimentation and grazing loss and are all easily measurable or obtainable from the literature (Weithoff, 2003). These traits relate to resource (i.e. nutrients, light) acquisition (traits 1-7), predator avoidance (traits 4-5, 7) and reproduction (trait 7) (Litchman and Klausmeier, 2008). The capacity for nitrogen fixation is a trait that enables acquisition of atmospheric nitrogen (e.g. some cyanobacteria) and provides a competitive advantage under nitrogen-limited conditions (Herrero and Flores, 2008). This was a binary variable in the trait matrix. The silica demand trait (also binary) was included because diatoms and some silicoflagellates need silica to build their frustules and

scales (Lee, 1999). Silica also influences functioning of the community as it increases the plankton's specific weight, especially in diatoms, leading to higher sedimentation rates (Reynolds, 1984). The mixotrophy (binary) trait is related to the ability to feed in both heterotrophic and autotrophic modes (Raven, 1997) and confers an advantage under nutrient-poor conditions (Bird and Kalff, 1987; Laybourn-Parry, Marshall and Marchant, 2005). The trait of the tendency to form chains or colonies is particularly relevant for phytoplankton, as it determines susceptibility to zooplankton grazing and affects nutrient acquisition and cell sinking rates (Grover, 1989). Cell motility (categorical variable) may be an asset in environments exhibiting marked nutrient gradients such as stratified lakes, where motile organisms can migrate towards favourable conditions and form patches as well as counteract sedimentation (Clegg, Maberly and Jones, 2007; Visser *et al.*, 1996). Three motility categories were assigned: non-motile cells, buoyancy regulation through gas vacuoles, and flagellated species (three-dimensional motility). Pigment composition is a key trait that characterizes phytoplankton ability to capture different parts of the visible light spectrum, as well as different light intensities (Falkowski and Raven, 1997; Stomp *et al.*, 2004). The pigment composition of the peripheral antennae of four main spectral groups were used: green containing Chl *a*, Chl *b* and xanthophyll, blue with phycocyanin, brown with Chl *a*, Chl *c* and xanthophyll (fucoxanthin or peredinin), and mixed with Chl *a*, Chl *c* and phycoerythrin. Information required for the first six traits was obtained from the literature. The final trait, cell size, is relate to growth rate (Banse, 1976; Sommer, 1981), zooplankton edibility (Gliwicz, 1977; Lampert *et al.*, 1986), sinking rate (Ptacnik, Diehl and Berger, 2003) as well as nutrient uptake (Grover, 1989; Smith and Kalff, 1982) and was estimated based on the longest linear dimension (LLD) of the cell. LLD is a continuous trait and mean values across all lakes for each species were used based on measurements of about 20 cells per species from each lake ($\leq$ 5 cells in rare species).

Using the functional traits, a community dendrogram based on Gower's distances between each pair of species was estimated for the species found in all the studied lakes. The dendrogram was created using the unweighted pair-group clustering method with arithmetic averages (UPGMA method). The FD of each lake was then calculated as the sum of dendrogram branch lengths of only those species found therein (Petchey and Gaston, 2002, 2006). All FD measures were calculated using R2.20 and code obtained from O. Petchey's

website (*http://owenpetchey.staff.shef.ac.uk/Code/Code/calculatingfd.html*). We modified their routine to use Gower's distance instead of the Euclidean distance, as this is more appropriate for our mixed (discrete + continuous) traits (Podani and Schmera, 2006, 2007).

3.2.7 Total zooplankton biomass

Total zooplankton biomass (Zoo biomass) was measured to test a potentially top-down effect of zooplankton on phytoplankton diversity. Zooplankton vertical net hauls were taken using a 0.5 m diameter, 2 m long, 100 μm mesh net from 1 m above the sediment of the lake surface. Samples were collected and preserved in 75% ethanol. Subsamples from each preserved zooplankton sample were passed through a Laser Optical Plankton Counter (LOPC, Brooke Ocean Technology, Darmouth, Nova Scotia; Herman, Beanlands & Phillips, 2004) lab benchtop version to count and size particles. More details on the zooplankton analysis with the LOPC can be found in Finlay *et al.* (Finlay, Beisner and Barnett, 2007).

3.2.8 Statistical analyses

One-way Analysis of Variance (ANOVA) followed by Tukey tests were used to test for differences in mean relative integrated biomass of each phytoplankton taxon over time (June vs. July vs. September).

Differences between months in mean values of phytoplankton vertical distribution (depth of biomass maxima and CV of total Chl *a*) were tested using ANOVA and Tukey tests. To identify and compare environmental factors that accounted for the greatest variation in the depth of biomass maxima and CV of total Chl *a* across lakes, ANCOVA with month as a covariate was used. Differences between months and phytoplankton spectral groups in mean values of vertical distribution (depth of biomass maxima and CV of biomass) were tested using a two-factor ANOVA and Tukey tests, with month and group as the fixed factors Relationships between environmental variables and spectral groups in each sampled month were further analyzed using redundancy analysis (RDA). All variables were centred and standardized prior to ordination. Significant predictor variables were determined using forward selection and significance was assessed with Monte Carlo permutation (999 permutations). Multivariate analysis of covariance (MANCOVA) was used to compare

regressions between environmental variables and phytoplankton spectral groups from the contrasted months.

ANOVA and Tukey tests were used to assess the differences between months in the mean values of phytoplankton diversity (S, H' and FD). To identify and compare environmental factors that accounted for the greatest variation in the phytoplankton diversity variables across lakes, ANCOVA with month as a covariate was used.

Independent variables tested in the ANCOVAs, RDAs and MANCOVAs were those related to lake morphometry (i.e. Z_{max} and fetch), chemistry (i.e. TP, TN: TP, A_{440}), physical habitat structure variables (Z_{Secchi}, Z_{thermo}, CV temp. and RTR) and total zooplankton biomass (only for the ANCOVAs on diversity measures). RDAs were performed using CANOCO version 4.5 (ter Braak, 1990) and the other statistical tests were done using JMP 8.0 (SAS Institute Inc. 2008) at an $\alpha = 0.05$ level of significance. Variables with non-normal distributions were arcsine-square root transformed (for the relative biomass of different phytoplankton taxa), or log-transformed for all other variables, prior to analysis. Prior selection of independent variables was made to exclude those that had correlations of > ±0.75.

3.3 Results

3.3.1 Community composition

Based on the microscope counts integrating across the photic zone of the water column, phytoplankton communities in June consisted mainly of diatoms (on average 44% of total biomass) followed by chrysophytes (17%) and cryptophytes (15%) (Fig. 3.1). In July, diatoms, chrysophytes, cryptophytes and cyanobacteria were all dominant (23%, 21%, 19% and 18%, respectively) whereas in September cryptophytes and cyanobacteria were co-dominant (both 29%) follow by diatoms and chrysophytes (17% and 13%, respectively). The other taxa contributed on average ≤12% of total biomass. Overall patterns of decline with time were observed for diatoms and dinoflagellates; increases over time for cryptophytes and cyanophytes; while mid-summer peaks in relative biomass occurred in chrysophytes and chlorophytes. Statistically, relative biomass of diatoms was significantly higher in June than in the other two sampled months (ANOVA, $P < 0.0001$) whereas biomass of cryptophytes

and cyanobacteria were significantly higher in September than in June (P = 0.0046 and P = 0.0082, for cryptophytes and cyanobacteria, respectively).

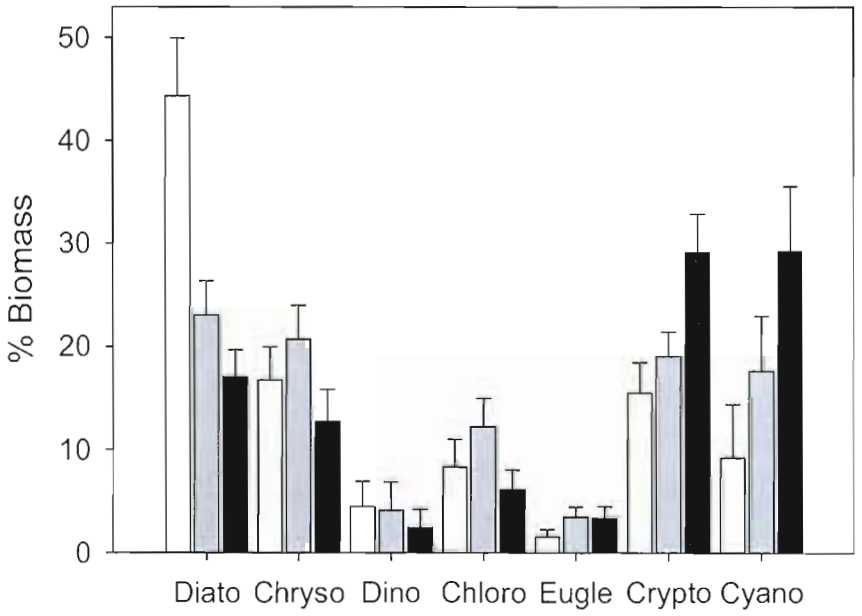


Fig. 3.1. Relative biomass of the different phytoplankton taxonomic groups: diatoms (diato), chrysophytes (chryso), dinoflagellates (dino), chlorophytes (chloro), euglenophytes (eugle), cryptophytes (crypto) and cyanobacteria (cyano) in June (white bars), July (grey bars) and September (black bars).

3.3.2 Vertical structure of total chlorophyll *a*

Oligo-mesotrophic lakes were those that had one or more peaks in Chl *a* whereas shallow and highly eutrophic lakes were most commonly the ones that had no clear peaks. Single peaks in total Chl *a* were observed in at least half of the lakes in each time period (sixteen, twelve and nine lakes in June, July and September, respectively). Four lakes had a second peak in July (Lakes Bowker, Fitch, Lyster and Parker) and in September (Lakes

Fraser, Lovering, Lyster and Parker) whereas only the Lake Simoneau showed a third peak (in September). The most eutrophic lake (Tomcod) never had obvious peaks. For the other shallow eutrophic lakes, Lake St. Georges had a peak only in July, while Lake Waterloo had one only in June. The deeper Lake Brome showed peaks in June and July but not in September.

The depth of maximum Chl *a* across the three sampled time periods was widely variable across all lakes, ranging from depths of 0.1 m to 15.8 m (Table 3.1). Mean Chl *a* depth did not differ by month (ANOVA, $P = 0.5848$). Depth of Chl a_{max} was negatively related to TP concentration (Fig. 3.2A) (ANCOVA, $P < 0.0001$, $R^2_{adj.} = 0.69$, Table 3.2). However for the two other environmental variables (Z_{max} and fetch) that were significantly related to the depth of the Chl a_{max} (Table 3.2), there was a statistically significant effect of month (Fig. 3.2B, C). Comparison of the slopes of the log-log relationships between Chl a_{max} depth and Z_{max} indicated that the depth of Chl a_{max} increased with lake depth faster in July than at the other times (slopes = 0.78, 0.93 and 0.81 in June, July and September, respectively) (Fig. 3.2B). Overall however, Chl a_{max} in June was deeper than in September across all lakes but deeper only in shallow lakes relative to July (Fig. 3.2B). Depth of the Chl a_{max} increased with fetch in June, but decreased with fetch in July and showed no relationship in September but none of the partial regressions were significant (slopes= 0.39, -0.19 and 0.07 in June, July and September, respectively) (Fig.3.2C).

CV of total phytoplankton biomass ranged between 0.03 and 0.96 (Table 3.1) with no differences in mean CVs between months (ANOVA, $P = 0.1571$). The CV of total Chl *a* was positively related only to vertical temperature variation (CV temp.) (Table 3.2), with no effect of time on the relationship (ANCOVA, $P < 0.0001$, $R^2_{adj.} = 0.32$).

3.3.3 Vertical structure in different phytoplankton spectral groups

In GREENs, BROWNs and CRYPTOs showed deepest maxima in June and July while CYANOs were at their deepest in September. GREENs and CYANOs were generally found at shallowest depths except for CYANOs in September (Fig. 3.3A). However, these differences between months and between spectral groups in the depth of maximum biomass were not statistically significant (2-factors ANOVA, $P = 0.5848$).

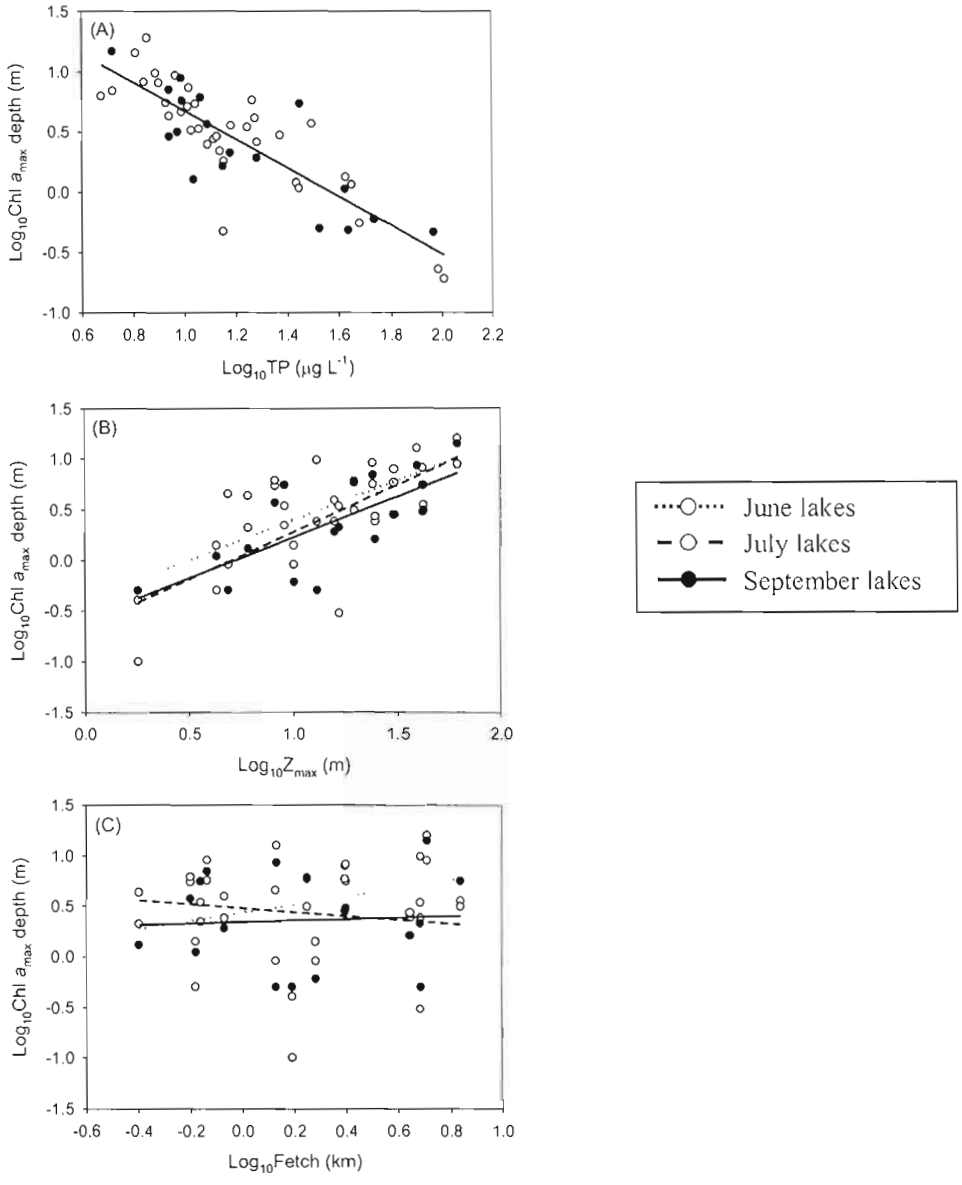


Fig. 3.2. Partial regression plots from a model relating the depth of maximum chlorophyll *a* (Chl a_{max} depth) to (A) epilimnetic total phosphorus (TP), (B) maximum lake depth (Z_{max}) and (C) fetch for all studied lakes from June (white circles), July (grey circles) and September (black circles). Plotted lines for significant different relationships between months are: dotted, dashed and solid for June, July and September, respectively. All variables were $\log_{10}$ transformed.

Table 3.2
Results of ANCOVAs between phytoplankton distribution-related variables [depth of maximum chl *a* (Chl a_{max} depth) and the coefficient of variation of the chl *a* (CV chl *a*)], testing for monthly differences in environmental driving variables

	Coefficient (SE)	*P*	P_{global}	$R^2_{adj.}$
Log_{10}Chl a_{max} depth				
Constant	1.7408 (0.1370)	<0.0001	<0.0001	0.69
Log_{10}TP	−1.0695 (0.1104)	<0.0001		
$Log_{10}Z_{max}$*Month	0.2268 (0.1507)	0.0348		
Log_{10}Fetch*Month	−0.3526 (0.1645)	0.0273		
Log_{10}CV chl *a*				
Constant	−0.1874 (0.0942)	0.0524	<0.0001	0.32
Log_{10}CV temp.	0.3783 (0.0774)	<0.0001		

Independent variables tested were mean and maximum depth, fetch, epilimnetic total phosphorus (TP), absorption at 440 nm, Secchi depth, thermocline depth, coefficient of variation of the temperature (CV temp.) and mean relative thermal resistance to mixing. All variables were log_{10} transformed. Only significant relationships ($P < 0.05$) were included. SE: standard error.

The RDA between the depth of biomass maxima (peaks) of the phytoplankton spectral groups and the environmental factors by month showed that absorption at 440 nm was the only significant environmental factor in June (Fig. 3.4A): peak CRYPTO biomass occurred more deeply in darker lakes (higher A_{440}), while BROWNs were deeper in clearer lakes (low A_{440}). In July, Z_{Secchi} and Z_{thermo} were both significantly related to peak biomass depths of the phytoplankton spectral groups (Fig. 3.4B). Shallower peaks of CYANOs and GREENs were favoured in clear lakes (high Z_{Secchi}). The second axis was related to thermocline depth with deeper thermoclines favouring deeper peaks in CRYPTOs. In September water clarity (Z_{Secchi}) was the only significant environmental factor (Fig. 3.4C). Again, low transparency favoured mainly deeper maxima in GREENs and CYANOs. Deeper peaks in BROWNs occurred in clear lakes as in June, while CRYPTO showed only a weak tendency to be affected by the light environment. The relationships between depth of maximum biomass of all four spectral groups and the environmental variables selected in the RDA's were all

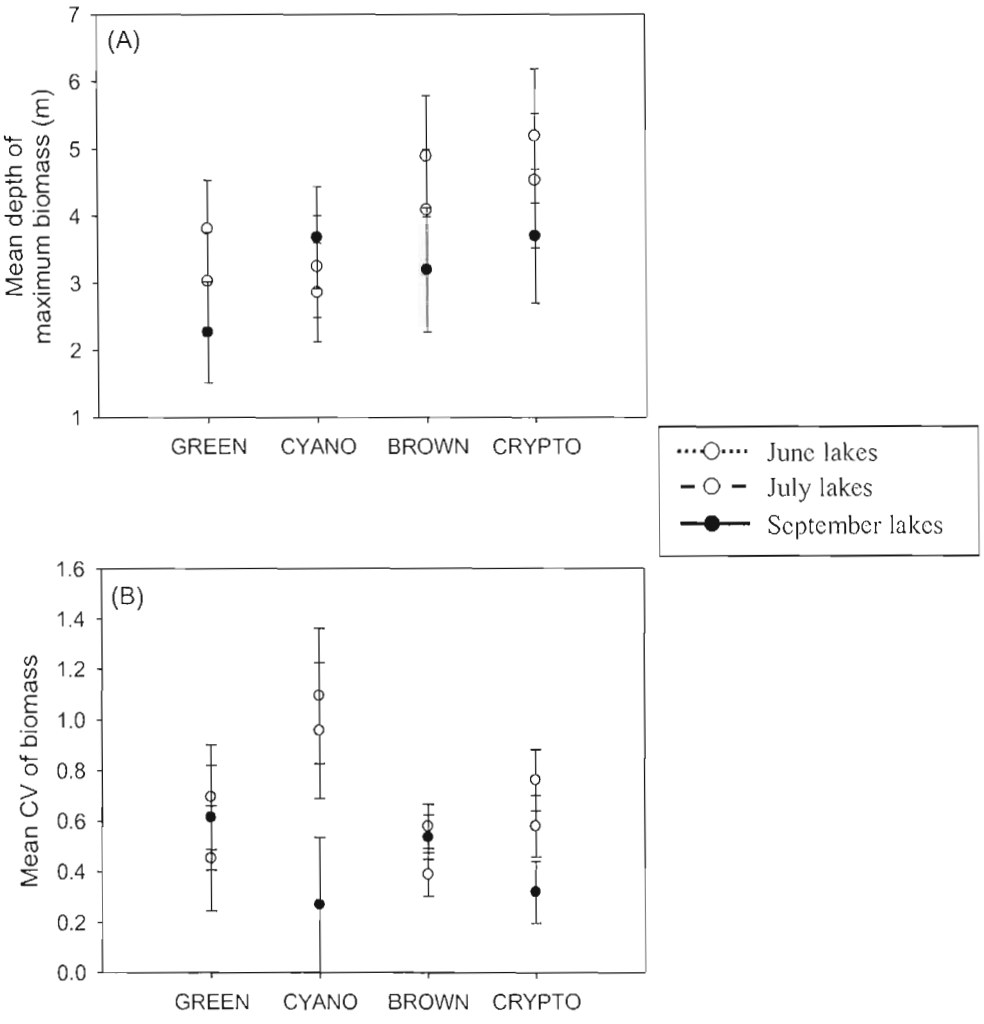


Fig. 3.3. Mean values of the (A) maximum biomass depth and (B) coefficient of variation (CV) of biomass of the different phytoplankton spectral groups (GREEN, CYANO, BROWN and CRYPTO) for all studied lakes from June (white circles), July (grey circles) and September (black circles).

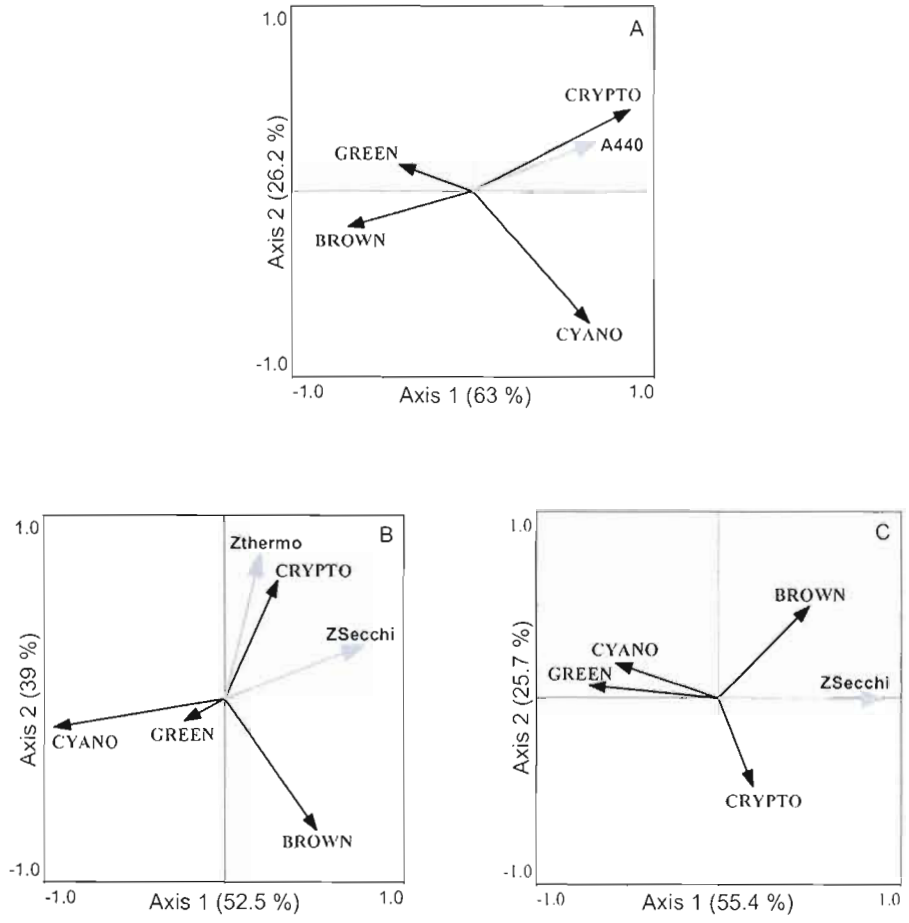


Fig. 3.4. Ordination biplots for the redundancy analysis (RDA) of the depth of maximum biomass from the different phytoplankton spectral groups and environmental variables for all studied lakes from June (A), July (B) and September (C). Black arrows represent the phytoplankton spectral groups and grey arrows represents the significant environmental factors that were selected by the RDA. Independent variables tested were maximum lake depth, fetch, epilimnetic total phosphorus, absorption at 440 nm (A_{440}), Secchi depth (Z_{Secchi}), thermocline depth (Z_{thermo}), coefficient of variation of the temperature and mean relative thermal resistance to mixing.

significantly different between months (MANCOVA whole model: Wilks' λ appr. F = 1.7446, P = 0.0069).

In June and July, heterogeneity (CV) in the water column biomass distribution was greatest in the CYANOs and lowest in the BROWNs while in September CYANOs along with CRYPTOs showed the least vertical variation (Fig. 3.3B). Significant differences were observed between months (2-factor ANOVA, P = 0.0015), with lower overall variation in September than in the other months, but not between spectral groups (P = 0.8343). Interaction could not be tested for because of a lack of replicate observations within months.

In June, the CRYPTO distribution had greatest vertical heterogeneity when the water column was least structured (low temperature variation) (RDA; Fig. 3.5A). The vertical variation in GREEN and BROWN distribution on the other hand, increased with greater vertical thermal structure (CV temp.). In July, the largest, deepest lakes (high wind fetch and Z_{max}) had the greatest heterogeneity in vertical distribution of GREENs but the lowest in CRYPTOs (Fig. 3.5B). In September, no environmental factors were significantly related to the heterogeneity distribution of phytoplankton spectral groups. These relationships were statistically different between months (MANCOVA whole model: Wilks' λ appr. F = 2.0722, P = 0.0118).

3.3.4 Phytoplankton diversity

Across all lakes, species richness (S), after rarefaction, varied from 7 to 23 (Table 3.1). Mean S was higher in July than in the other months (ANOVA, P = 0.005). Shannon diversity varied widely across all lakes (Table 3.1) and mean H' was significantly higher in July than in June (ANOVA, P = 0.0331). Functional diversity (FD) in most lakes ranged between 0.50 and 0.70 (Table 3.1) with no significant differences in mean FD between months (ANOVA, P = 0.101). Lakes with the highest FD (>0.70) were D'Argent in June, Brome and Fitch in July and St. Georges in September (data not shown). The lowest value of FD (=0.37) was observed in Lake Brome in June. The next lowest FD values (<0.50) included Lakes Lyster and Simoneau in June, Lake Bowker in July and Lakes Bowker, Lyster and Orford in September (data not shown).

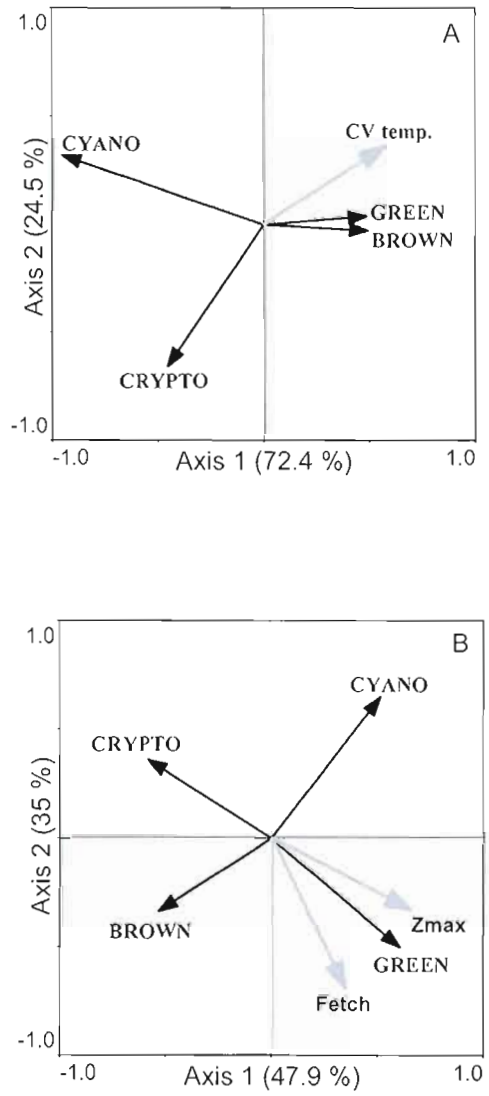


Fig. 3.5. Ordination biplots for the RDA of the coefficient of variation of the biomass from the different phytoplankton spectral groups and environmental variables for all studied lakes from June (A) and July (B). Black arrows represent the phytoplankton spectral groups and grey arrows represents the significant environmental factors that were selected by the RDA. Independent variables tested were maximum depth (Z_{max}), fetch, epilimnetic total phosphorus, absorption at 440 nm (A_{440}), Secchi depth, thermocline depth, coefficient of variation of the temperature (CV temp.) and mean relative thermal resistance to mixing.

Table 3.3
Results of ANCOVAs for the three phytoplankton diversity measures testing for monthly differences in environmental driving variables

	Coefficient (SE)	P	P_{global}	$R^2_{adj.}$
Log_{10}Species richness				
Constant	1.1803 (0.0138)	<0.0001	0.0059	0.18
Month (June+Sept. vs. July)	-0.0495 (0.0196)	0.0059		
Log_{10}Shannon index				
Constant	0.4065 (0.0334)	<0.0001	0.0308	0.07
Log_{10}CV temp.	0.0611 (0.0274)	0.0308		
Log_{10}Functional diversity				
Constant	-0.2428 (0.0080)	<0.0001	0.0021	0. 33
A_{440}	0.0723 (0.0218)	0.0035		
Month (June+Sept. vs. July)	-0.0228 (0.0109)	0.0203		
Log_{10}Zoo biomass*Month (June+Sept. vs. July)	0.0513 (0.0344)	0.0266		

Independent variables tested included maximum depth (Z_{max}), fetch, total phosphorus (TP), total nitrogen:total phosphorus (TN:TP), absorption at 440 nm (A_{440}), total zooplankton biomass (Zoo biomass), Secchi depth (Z_{Secchi}), thermocline depth (Z_{thermo}), coefficient of variation of the temperature (CV temp.) and relative thermal resistance to mixing (RTR). All variables were log_{10} transformed. Only significant relationships ($P < 0.05$) were included. SE: standard error.

The ANCOVA showed no significant relationships between S and the environmental factors but did show that the intercept in July was significantly greater than for the other months (ANCOVA, $P = 0.0059$, $R^2_{adj.} = 0.18$; Table 3.3). Shannon diversity was positively and weakly related only to CV temp. with no effect of month (ANCOVA, $P = 0.0308$, $R^2_{adj.} = 0.07$; Table 3.3). Functional diversity increased significantly with increasing water colour (A_{440}) and with zooplankton biomass (ANCOVA, $P = 0.0021$, $R^2_{adj.} = 0.33$; Table 3.3). However, the relationship with zooplankton changed with month ($P = 0.0266$; Table 3.3), with no significant relationship in July, and with similar increases in phytoplankton FD with increasing zooplankton biomass in June and September (slope: 0.15 and 0.09 for June and September, respectively).

3.4 Discussion

3.4.1 Community composition

In most of our lakes, changes in phytoplankton composition through the growing season followed the typical pattern predicted for dimictic temperate lakes (Sommer *et al.*, 1986). At the end of spring, diatoms and/or small flagellates (i.e. chrysophytes and cryptophytes) represented the largest portion of phytoplankton biomass in our lakes. At the height of summer in July, when stratification is strongest (highest CV temp. and RTR) in our region, there was a more mixed composition of phytoplankton, with an approximately equal biomass contribution of diatoms, chrysophytes, cryptophytes and cyanobacteria. We also observed greater species richness and diversity (H' and FD) in mid-summer. Towards autumn the physical environment of the phytoplankton changed, mixing depth increased, stratification became weaker and light penetration decreased. At this time, cyanobacteria and cryptophyte biomass was greatest across the lakes. Exceptions to this succession pattern were the shallowest lakes with high epilimnetic TP, which were always dominated by cyanobacteria (i.e.: Lakes Tomcod and Waterloo) or with a large chlorophyte biomass (i.e.: Lake St. Georges).

3.4.2 Phytoplankton distribution

The first major goal of this study was to assess patterns in the vertical distribution of phytoplankton communities with respect to lake environmental factors at three distinct time periods: late spring, mid-summer and early autumn. We expected deeper peaks in bulk phytoplankton biomass during periods when light penetration and wind speed were greater. We also expected greater variation in the spatial distribution of bulk phytoplankton when lake thermal structure was more heterogeneous (higher RTR and CV temp.), with the spectral groups expected to be differentially affected by changes of habitat structure across the season.

Mean peak depth of total phytoplankton biomass was deepest in June although not statistically different from the other months. At all times, the position of maximum Chl *a* biomass was shallower in high TP lakes. TP provides an estimate of primary production (standing crop) in lakes from this region (chap. 1; Giani *et al.*, 2005). Light absorbance and scattering by phytoplankton likely promoted light attenuation with depth (Mazumder *et al.*, 1990), thereby indirectly leading to a shallower peak depth. The depth of the peak in total phytoplankton was also positively related to maximum lake depth, although changes with depth were more pronounced in July. This latter result suggests that phytoplankton better reflect the dominant habitat structure (i.e. light penetration, thermocline depth) in mid-summer, at a time when physical conditions are more stable. The relationships in depth of Chl a_{max} with wind fetch, showed a trend of increasing in June, no change in September, and a slight decrease in July, although none of the partial regressions were significant. The relationship for June was the strongest, probably because wind speed was also highest at this time (ANOVA and Tukey test, $P < 0.0001$), allowing for a greater mixing effect. Strong wind mixing the water column in lakes with large fetch would have favoured a deeper accumulation of phytoplankton biomass. Furthermore at this time the communities were dominated by diatoms which would be especially susceptible to having their positions in the water column be driven by mixing. The weak or lack of relationship later in the season can be explained by lesser winds as well as by a community composition dominated by phytoplankton groups which are better able to modify their position in the water column (e.g.

cyanobacteria, cryptophytes and chrysophytes), irrespective of lake fetch (Clegg, Maberly and Jones, 2007; Visser *et al.*, 1996; Reynolds, 1984).

Heterogeneity of the bulk phytoplankton biomass distribution was greatest at mid-summer but, contrary to expectation (H1), these differences between months were not statistically different. Interestingly, regardless of month, the relationship between CV of Chl *a* and vertical temperature heterogeneity was always the same, suggesting conservatism in this relationship, as one might expect. Greater variation in phytoplankton biomass was observed in lakes with more heterogeneous habitats (high CV temp.), as predicted from theory (Klausmeier and Litchman, 2001) and previously found in lakes from this region (chap. 1).

Overall, for the spectral groups, the mean position of the peaks in biomass did not change over time, likely because of large variation around the means. However, their relationships with different environmental variables did change through time. Peak depths of spectral groups, were instead mainly related to *in situ* light-related factors such as water colour and transparency (the exception being Z_{thermo} in July), with idiosyncratic responses by group. Characteristics of the light environment were primordial factors related to the peak positions of the phytoplankton spectral groups, more so than thermal regime and moreso in the shoulder seasons than in mid-summer. Furthermore, the significant measures of the light environment changed from being simply water colour in June to both water colour and phytoplankton biomass (Secchi depth) later. On the other hand, overall vertical variation of spectral group biomasses did change through the season, with the least heterogeneity in September. Unlike for peak depths, vertical variation in the spectral groups was related to physical factors, specifically those characterizing lake morphometry and thermal structure but not light, in June and July. In September, none of the measured factors were relevant for vertical variation in spectral groups.

The chlorophytes (GREENs) showed shallow average peak depths and intermediate levels of heterogeneity in distribution across the growing season. Chlorophytes tend to saturate growth at higher irradiance than other microalgal classes and consequently, can tolerate very high light levels (Richardson, Beardall & Raven, 1983), such as those found near the surface of the lakes. Despite their ability to tolerate high light levels, in June, deeper

maxima in GREENs were found in lakes with clear waters. Meanwhile, the opposite pattern was observed in July and September when peak depths were mostly shallow in clearer waters. Heterogeneity in the distribution of GREEN biomass was greatest in lakes with high vertical temperature variation in June, as also observed for total Chl *a*, and also in large lakes in July when stratification was at its maximum. It appears that the variation in the distribution of GREENs is strongly affected by stratification but peak depths are more a function of tolerance for high irradiance levels.

The depth of maximum biomass of cryptophytes (CRYPTOs) is frequently found in the metalimnion of stratified lakes, as we also observed, where their low light and high nutrient requirements are both satisfied (chap. 1; Graham and Wilcox, 2000; Klaveness, 1988; Ptacnik, Diehl and Berger, 2003). In our study, cryptophytes generally had deep maxima compared to the other spectral groups. They had intermediate values of heterogeneity in June and July, but displayed a relatively homogeneous distribution at the end of summer. In late-spring, the deeper peaks of CRYPTO were found in lakes with darker waters, whereas in mid-summer they were deeper in lakes with deeper thermoclines. The preference of cryptophytes for low-light environments (Klaveness, 1988; Graham and Wilcox, 2000), for mixotrophy (Raven, 1997), as well as their ability to select by active motility, a favourable position in the water column (Clegg, Maberly and Jones, 2007) likely confer on them a competitive advantage in highly coloured (high DOC), low-light environments (Klug and Cottingham, 2001). However, towards autumn, cryptophytes together with cyanobacteria, were more homogeneously distributed than the other groups. Thus, changes in the physical environment at this time (i.e. weaker stratification with deeper mixing depth and lower light penetration) could have promoted a more homogeneous distribution.

The most diverse spectral group, the BROWNs showed relatively deep maxima, particularly in the two first sampled months and intermediate values of heterogeneity distribution in all months. Deeper peaks of BROWNs were observed in clear lakes whereas variability in their distribution increased with temperature heterogeneity but only in June. Based on microscope counts, the BROWN group in our study was mainly composed of diatoms and chrysophytes, while dinoflagellates contributed to only a small fraction of

biomass (≤ 7% of BROWN biomass). Because diatoms tend to sink and dominate under low-light conditions, their peaks are expected to be near the metalimnion in well-stratified, relatively calm waters (Reynolds, 1984; Litchman, 1998; Jäger, Diehl & Schmidt, 2008). On the other hand, chrysophytes show affinity for moderate light levels and their flagella allow them to select and maintain favourable positions throughout the water column (Clegg, Maberly and Jones, 2007). The fact that we mostly detected the BROWNs in metalimnetic peaks suggests that these peaks are probably dominated by diatoms, while the chrysophytes are less abundant and/or more diffusely distributed, without major peaks.

Finally, cyanobacteria (CYANOs) showed shallow peaks with a heterogeneous distribution in June and July but a more homogeneous distribution through the water column in September. This group was particularly dominant in shallow lakes with high TP, such as Lakes Tomcod and Waterloo. In July and September, peak depths of cyanobacteria were closely related to light penetration. In early autumn, this group together with cryptophytes were so dominant (on average 58% of total biomass) that their biomass was probably the major factor leading to darker waters both because of shading through their biomass, and because of greater DOC release which would reduce light penetration.

3.4.3 Phytoplankton diversity

The second major goal of our study was to evaluate temporal patterns in phytoplankton diversity with respect to lake environmental factors. We calculated diversity using two taxonomically-based indices (species richness and the Shannon index), as well as one functional index (FD), in order to determine whether the patterns in these different measures responded in a similar way to lake habitat structure across the three distinct time periods. We predicted that phytoplankton diversity would be higher in periods with more spatially heterogeneous habitats (i.e. lakes with greater vertical temperature variation).

As hypothesized in H3, the means of each diversity index (i.e. species richness, Shannon index and functional diversity) differed between months, with higher values at mid-summer that were statistically different only for the species measures (S and H') and not for the functional one (FD). In mid-summer in our lakes, CV of temperature and thermal resistance to mixing were higher, and light penetration was greater than at other times.

Therefore, the higher species diversity observed at mid-summer can be attributed to a greater habitat heterogeneity offering several niches available for the phytoplankton as predicted. In July, there was a more mixed composition of phytoplankton, but despite a wider range in the cell size trait (data not shown), functional differences were not great enough to affect FD.

In contrast to mean differences, FD showed variation with more environmental variables that was stronger ($R^2_{adj.}$) than for the species diversity indices. In particular H' increased only with higher vertical temperature variation in the photic zone. Thus, Shannon diversity, which reflects both richness and evenness, was higher in lakes with greater vertical heterogeneity. In such lakes, we would expect the existence of a vertical spectrum of niches in the water column (Clegg, Maberly and Jones, 2007; Reynolds, 1984) allowing a maintenance of a greater diversity (Jäger, Diehl and Schmidt, 2008; Stomp *et al.*, 2007). On the other hand, FD was influenced both by water colour and zooplankton biomass, although this latter relationship was variable between months. Mixotrophic species are more frequently present in lakes with coloured waters (Klaveness, 1998), increasing the number of functional traits in these lakes. FD was positively related to zooplankton biomass in spring and fall but showed no relationship in mid-summer. Higher zooplankton biomass in June and September, probably promoted a variety of predator-evasion strategies in phytoplankton, such as very small or very large body sizes and high motility organisms, leading to a higher FD; although this hypothesis requires further exploration.

3.5 Conclusion

In summary, it appears that in most lakes, changes in phytoplankton composition through the season followed the typical pattern predicted for temperate northern lakes, with some exceptions. In late spring, when diatoms and/or small flagellates represented the largest portion of phytoplankton biomass in our lakes, mean peak depth of total phytoplankton biomass was deeper than in the other months, probably favoured by the strongest wind effects during this period. In mid-summer, when stratification was strongest and most stable (highest CV temp. and RTR), we observed a greatest species richness and diversity (H' and FD), as well as a more heterogeneous distribution of phytoplankton biomass. Moreover, S and FD did not have the same relationship to the environmental variables in July as in the other months, being at this time negatively related to maximum lake depth, suggesting that phytoplankton

better capture or reflect the physical lake structure (i.e. light penetration, thermocline depth) under more stable physical conditions. Towards autumn, stratification became weaker, mixing depth increased, and light penetration decreased. At this time, the dominant groups, cyanobacteria and/or cryptophytes, showed a more homogeneous biomass distribution through the water column.

CONCLUSION

Les facteurs qui contrôlent la distribution et la diversité du phytoplancton dans les lacs sont nombreux, incluant entre autres l'hétérogénéité spatiale. Cette hétérogénéité dans la colonne d'eau d'un lac peut se traduire par des gradients verticaux de température ou des ressources nécessaires à la croissance du phytoplancton comme la lumière ou les nutriments. Dans les lacs tempérés de l'Hémisphère Nord, la thermocline estivale constitue une des principales structures physiques de la colonne d'eau susceptible d'affecter le phytoplancton. De ce fait, l'objectif général de cette thèse était d'établir pour un ensemble de lacs les patrons dans la distribution verticale et la diversité du phytoplancton, et leurs relations avec la structure physique de la colonne d'eau. Afin d'atteindre cet objectif, 45 lacs du Sud du Québec (Canada) montrant des variations importantes de taille, de concentration d'éléments nutritifs et de couleur de l'eau ont été étudiés durant la période de stratification estivale.

Du fait que la structure physique d'un lac, en termes de température et de lumière, peut avoir une influence sur la distribution et la diversité du phytoplancton, le premier objectif spécifique était d'identifier les facteurs qui prédisent le mieux la structure de l'habitat pour le phytoplancton, où l'habitat est défini par la pénétration de la lumière, la profondeur de la thermocline, l'hétérogénéité dans la distribution verticale de la température [coefficient de variation de la température (CV temp.)] et la résistance thermique relative (RTR) au mélange de la colonne d'eau. Les résultats montrent que, dans l'ensemble, les lacs dont l'eau était plus colorée (absorption à 440 nm plus élevée) présentaient une colonne d'eau plus stable (une plus grande RTR au mélange), et quand la concentration de Chl *a* était également élevée la pénétration de la lumière était réduite et la thermocline moins profonde. Dans les lacs où le fetch était plus important, la thermocline était plus profonde et la variation verticale de la température plus faible.

Le second objectif spécifique était de déterminer comment la structure physique de la colonne d'eau affecte la distribution de la biomasse de phytoplancton. Afin d'atteindre cet objectif, le coefficient de variation verticale et la profondeur du maximum de biomasse totale et des différents groupes spectraux de phytoplancton ont été mesurés. Les groupes de phytoplancton examinés étaient limités à ceux mesurables par un spectrofluoromètre

submersible, qui permet la détection à très fine échelle spatiale de la biomasse des cyanophytes, des algues brunes (diatomées, chrysophytes et dinoflagellés), des algues vertes (chlorophytes) et des cryptophytes. Les résultats ont montré que, pour l'ensemble des lacs, des gradients de température prononcés favorisaient la distribution de la biomasse de phytoplancton dans des couches plus définies, alors que le maximum de biomasse était moins profond dans les lacs présentant une distribution verticale de la température plus homogène et des eaux plus colorées avec une concentration de phosphore total dans l'épilimnion plus élevée. D'autre part, la profondeur du maximum de biomasse et l'hétérogénéité des groupes spectraux de phytoplancton étaient principalement reliées à la couleur de l'eau et à la concentration de phosphore total dans l'épilimnion mais avec des réponses différentielles par groupe.

Afin de vérifier si les tendances observées étaient robustes, des lacs de deux régions voisines du Sud du Québec présentant des caractéristiques différentes, notamment en termes de couleur de l'eau et d'exposition au vent, ont été examinés. Dans les lacs de la région des Laurentides, la contribution du carbone organique dissous coloré au coefficient d'extinction de la lumière est beaucoup plus élevée, les valeurs de fetch généralement plus faibles et l'exposition au vent plus limitée que dans les lacs de la région de l'Estrie. Ainsi, l'objectif était d'abord de caractériser la structure physique de la colonne d'eau dans les lacs de ces deux régions puis de comparer leurs relations entre la distribution du phytoplancton et l'hétérogénéité physique de la colonne d'eau. La structure de l'habitat du phytoplancton était relativement différente entre ces deux régions contrastées. Dans l'ensemble, les lacs des Laurentides montraient une thermocline moins profonde, une plus grande variabilité dans la distribution de la température ainsi qu'une une RTR au mélange plus élevée que dans les lacs de l'Estrie. Les différences dans la structure de l'habitat se sont traduites par des différences dans l'hétérogénéité de la distribution du phytoplancton avec une distribution plus hétérogène de la biomasse totale de phytoplancton et des quatre groupes spectraux dans les Laurentides. La profondeur du maximum de biomasse totale et des groupes spectraux de phytoplancton était similaire dans les deux régions, à l'exception d'un maximum de biomasse des algues vertes plus profond dans l'Estrie, ce qui suggère des différences dans la composition taxonomique de ce groupe entre les deux régions.

Suite à l'identification des facteurs qui affectent la distribution du phytoplancton, les patrons de diversité des communautés phytoplanctoniques dans le même ensemble de lacs ont été évalués au regard des facteurs environnementaux qui définissent la présence et la persistance des niches disponibles pour le phytoplancton dans la colonne d'eau. Afin de déterminer si les différentes mesures de diversité répondaient de façon similaire à la structure de l'habitat, la diversité a été mesurée avec deux indices s'appuyant sur la taxonomie [la richesse en espèces (*S*) et l'indice de Shannon (*H*')] et un indice de diversité fonctionnelle (FD). Les résultats ont montré que dans les colonnes d'eau présentant une plus grande hétérogénéité verticale de la température mais sujettes au mélange par le vent (RTR plus faible), *S* et *H*' étaient plus élevés. Les valeurs de *H*' diminuaient également avec la concentration de phosphore total dans l'épilimnion. Cependant, la relation la plus simple et la plus forte a été trouvée pour FD avec la profondeur maximale du lac, ce qui reflète une réponse à une variable qui intègre d'autres variables physiques (p. ex. le CV temp. et la RTR au mélange).

Afin de vérifier si les tendances observées dans la diversité étaient robustes, les lacs des Laurentides et de l'Estrie ont également été comparés. La richesse en espèces dans les lacs montrait peu de variation entre ces deux régions contrastées et les facteurs reliés à *S* ne variaient pas entre les régions. D'autre part, les valeurs de *H*' et de FD montraient une diminution avec la profondeur maximale du lac dans l'Estrie, alors qu'une relation opposée était obtenue dans les Laurentides. La profondeur du lac, qui reflète l'hétérogénéité et la stabilité de l'habitat du phytoplancton, a conduit à ces différences interrégionales dans la diversité. Les lacs peu profonds des Laurentides, qui présentaient une distribution verticale de la température plus homogène et une colonne d'eau plus stable car bien protégés du vent, disposaient probablement de moins de niches disponibles pour le phytoplancton. Par conséquent, ces lacs montraient de plus faibles valeurs de *H*' et de FD, avec la dominance d'un petit nombre d'espèces et une variance de traits plus faible. En revanche, les lacs peu profonds de l'Estrie, plus exposés au vent, montraient quant à eux de plus fortes valeurs de *H*' et de FD. Une plus grande variation dans les traits, notamment concernant la fixation d'azote, la demande en silice, la composition en pigments et la taille des cellules a été observée et ces traits étaient plus équitablement répartis entre les espèces des lacs de l'Estrie.

Le dernier objectif était d'évaluer les tendances dans la distribution, la composition et la diversité dans les communautés de phytoplancton lors de variations de la thermocline estivale. Afin d'atteindre cet objectif, 18 lacs Sud du Québec montrant des gradients prononcés dans leur morphométrie, leur productivité et leur couleur de l'eau ont été examinés lors de trois périodes distinctes : le printemps tardif, la mi-été et le début de l'automne. Dans la plupart des lacs, les changements à travers la saison dans la composition du phytoplancton suivaient le patron typique prédit pour les lacs dimictiques tempérés de l'Hémisphère Nord. Les exceptions concernaient les lacs moins profonds et plus eutrophes toujours dominés par les cyanobactéries ou les chlorophytes. À la fin du printemps, lorsque les diatomées et/ou les petits flagellés représentaient la plus forte proportion de la biomasse de phytoplancton, le maximum de biomasse totale de phytoplancton était en moyenne plus profond que dans les autres périodes étudiées, probablement du fait de vents plus forts à cette période. À la mi-été, quand la stratification était plus prononcée et plus stable (CV temp. et RTR plus élevés), une plus grande richesse en espèces et diversité (H' et FD) ont été observées de même qu'une distribution plus hétérogène de la biomasse de phytoplancton. De plus, S et FD n'ont pas montré la même relation avec les variables environnementales à la mi-été que dans les autres périodes pendant lesquelles S et FD étaient reliés négativement à la profondeur maximale du lac, ce qui suggère une meilleure capacité du phytoplancton à saisir ou refléter la structure physique du lac (p. ex. la pénétration de la lumière et la profondeur de la thermocline) dans des conditions physiques plus stables. Vers l'automne, la stratification s'est affaiblie, la profondeur de la couche de mélange a augmenté et la pénétration de la lumière diminué. La biomasse des groupes dominants (cyanobactéries et/ou cryptophytes) montrait à cette période une distribution plus homogène le long de la colonne d'eau.

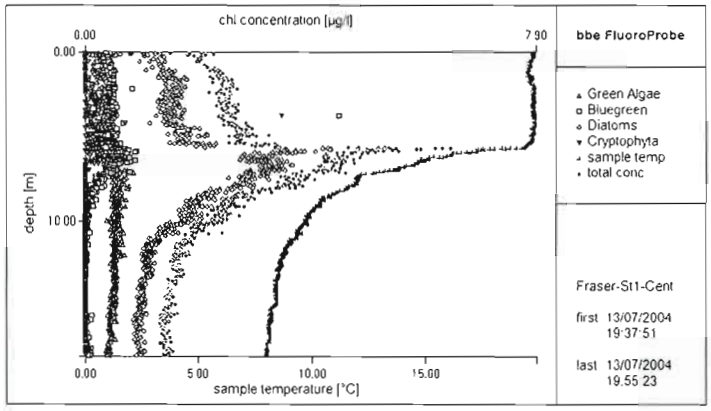
En conclusion, cette étude montre que l'hétérogénéité de la colonne d'eau durant la période de stratification estivale dans les lacs tempérés joue un rôle fondamental dans la distribution verticale et la diversité du phytoplancton. Une colonne d'eau plus hétérogène favorise la distribution en couches du phytoplancton et une augmentation de leur diversité. De plus, l'indice de diversité fonctionnelle s'est révélé être une mesure de la diversité montrant des réponses plus simples et plus fortes aux différents gradients environnementaux que les indices taxonomiques traditionnels.

Ultérieurement, il serait pertinent d'examiner plus largement les relations entre les variables environnementales et la diversité fonctionnelle dans d'autres types de lacs (ex. dans les lacs polymictiques tropicaux, les lacs monomictiques froids, etc.), ainsi que l'impact que les changements dans la diversité fonctionnelle peuvent avoir sur le fonctionnement de l'écosystème, notamment sur la production primaire et la respiration. De plus, il serait intéressant d'explorer le rôle du zooplancton (ex. broutage, migration, etc.) sur la distribution verticale du phytoplancton (ex. position du pic de la biomasse) ainsi que les relations entre la diversité fonctionnelle du phytoplancton et du zooplancton dans différentes conditions environnementales.

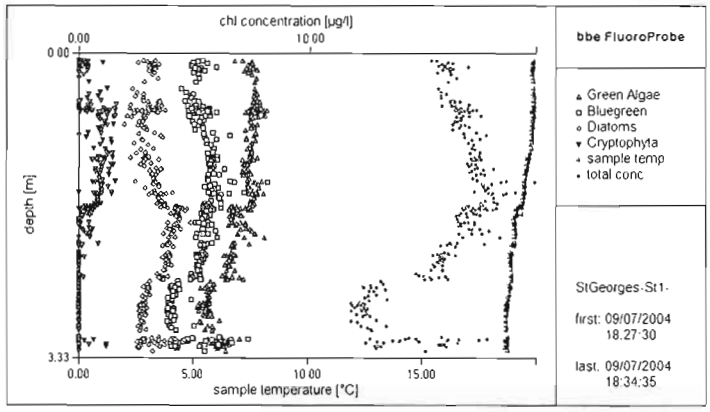
APPENDICE A

REPRESENTATIVE FLUOROPROBE PROFILES FOR TWO TYPICAL LAKES FROM THE EASTERN TOWNSHIPS (STRATIFIED LAKE FRASER AND WELL MIXED, SHALLOW LAKE ST. GEORGES) AND THE LAURENTIANS REGIONS (STRATIFIED LAKE MORENCY AND WELL MIXED, SHALLOW LAKE WALFRED).

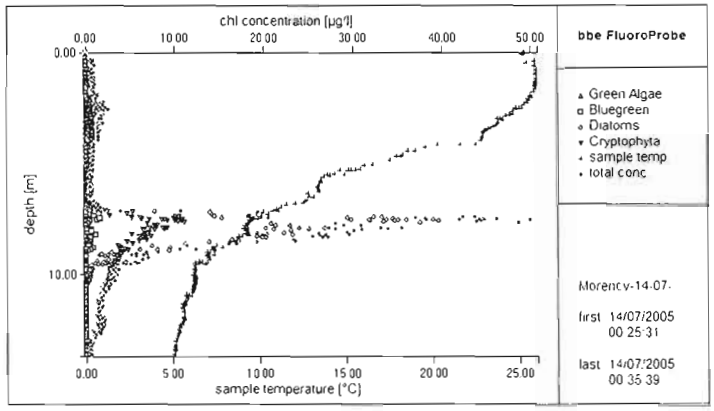
Lake Fraser



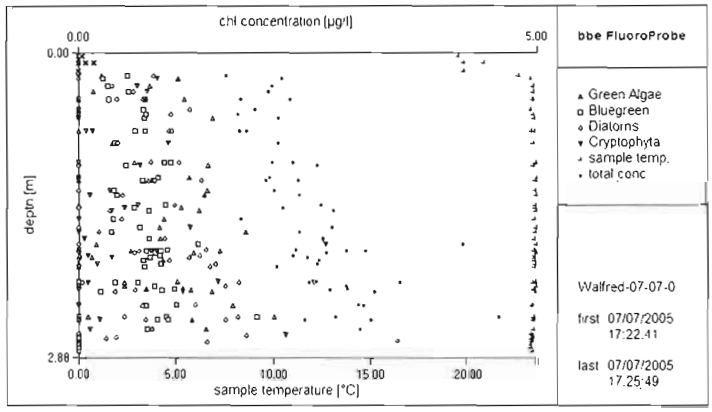
Lake St. Georges



Lake Morency



Lake Walfred



APPENDICE B

LAKE TROPHIC STATUS, PRESENCE OF STRATIFICATION (S), MAXIMUM DEPTH (Z_{max}), TOTAL PHOSPHORUS (TP) AND DISSOLVED ORGANIC CARBON (DOC) CONCENTRATIONS IN THE EPILIMNION (^{e}) AND THE HYPOLIMNION (^{h}) FOR A SUBSET OF LAKES FROM THE EASTERN TOWNSHIPS AND LAURENTIANS REGIONS SAMPLED IN THE SAME SUMMER AS WERE OTHER VARIABLES IN THIS STUDY.

Lake	Trophic status	S	Z_{max} (m)	TP ($\mu g\ L^{-1}$)	DOC ($mg\ L^{-1}$)
Eastern Townships Region					
Bowker	oligotrophic	Yes	61.90	7.29^{e} 6.70^{h}	2.18^{e} 2.05^{h}
Brome	meso-eutrophic	Yes	13.10	14.25^{e} 13.61^{h}	5.19^{e} 4.35^{h}
Brompton	oligotrophic	Yes	42.40	9.26^{e} 10.69^{h}	6.06^{e} 5.60^{h}
D'Argent	mesotrophic	Yes	15.90	12.51^{e} 13.72^{h}	7.73^{e} 6.19^{h}
Fitch	mesotrophic	Yes	16.70	14.00^{e} 16.33^{h}	4.33^{e} 3.88^{h}
Fraser	oligo-mesotrophic	Yes	19.80	11.24^{e} 11.97^{h}	5.58^{e} 5.54^{h}
Lovering	mesotrophic	Yes	25.00	14.68^{e} 12.11^{h}	7.09^{e} 6.81^{h}
Orford	oligotrophic	Yes	39.50	5.96e 4.98h	3.78e 3.11h
Parker	eutrophic	Yes	9.14	19.82^{e} 29.08^{h}	8.83^{e} 8.70^{h}
Simoneau	oligotrophic	Yes	24.40	7.87^{e} 12.70^{h}	4.79^{e} 3.98^{h}

St. Georges	eutrophic	No	4.30	43.78[c] 49.28[h]	7.76[c] 8.04[h]
Stukely	oligotrophic	Yes	30.50	5.99[c] 5.26[h]	4.69[c] 4.65[h]
Trois Lacs	eutrophic	Yes	10.10	26.54[c] 30.27[h]	9.35[c] 9.27[h]
Waterloo	eutrophic	No	4.90	33.30[c] 37.22[h]	7.35[c] 8.00[h]
Laurentians Region					
Achigan	oligo-mesotrophic	Yes	26.40	6.00[c] 9.33[h]	3.87[c] 3.32[h]
Connelly	oligo-mesotrophic	Yes	20.80	8.10[c] 10.56[h]	4.96[c] 3.57[h]
Ludger	oligo-mesotrophic	Yes	16.70	7.31[c] 10.21[h]	5.92[c] 4.52[h]
Montagne-Noire	oligotrophic	Yes	33.80	4.65[c] 6.65[h]	1.98[c] 1.62[h]

TP and DOC values of lakes Fraser, Lovering, Parker, Simoneau, St. Georges and Trois Lacs from Eastern Township Region and all lakes from Laurentians Region are unpublished data from S. Beauvais, Y. Prairie and P. del Giorgio (University of Quebec at Montreal) and R. Carignan (University of Montreal) respectively.

APPENDICE C

MAXIMMUM DEPTH (Z_{max}), EVENESS (J'), SHANNON DIVERSITY (H'), FUNCTIONAL DIVERSITY (FD), DOMINANT SPECIES COMPOSITION (75-80% OF TOTAL BIOMASS) AND FUNCTIONAL TRAITS FOR A SUBSET OF REPRESENTATIVE SHALLOW AND DEEP LAKES FROM THE EASTERN TOWNSHIPS AND LAURENTIANS REGIONS

Z_{max} (m)	J'	H'	FD	Dominant species	Functional traits
Eastern Townships Region					
Shallow lakes with high FD					
Baldwin					
8.23	0.81	2.83	0.70	*Mallomonas caudata* (16%)	Nitrogen fixation (3%)
				Chlamydomonas pseudopertyi (13%)	Si demand (27%)
				Tabellaria fenestrata (9%)	Mixotrophy (30%)
				Crucigenia tetrapedia (7%)	Chains/colonies (48%)
				Cryptomonas erosa (7%)	Buoyancy (3%)- flagellated (39%)
				Erkenia subaequiciliata (6%)	Green (42%)- brown (36%)- blue (12%)- mixed (9%)
				Fragilaria crotonensis (5%)	Cell size: 21 (1.5-105)*
				Mallomonas majorensis (5%)	
				Rhodomonas minuta (5%)	
				Staurastrum sp. (5%)	
Des Monts					
6.10	0.83	2.69	0.66	*Erkenia subaequiciliata* (16%)	Nitrogen fixation (0%)
				Dinobryon sertularia (14%)	Si demand (15%)
				Trachelomonas hispida (14%)	Mixotrophy (62%)

					Chroomonas norsdstedtii (9%)	Chains/colonies (31%)
					Uroglena europhaea (8%)	Buoyancy (0%)- flagellated (62%)
					Mallomonas caudata (5%)	Green (31%)- brown (38%)- blue (8%)- mixed (23%)
					Cryptomonas marssonii (4%)	Cell size: 22 (4-82)*
					Rhodomonas minuta (4%)	
					Cosmarium depressum (4%)	
Fitch						
	16.70	0.78	2.82	0.76	*Fragilaria crotonensis* (13%)	Nitrogen fixation (5%)
					Staurastrum gladiosum (13%)	Si demand (30%)
					Cryptomonas erosa (10%)	Mixotrophy (35%)
					Oscillatoria agardhii (10%)	Chains/colonies (46%)
					Cyclotella meneghiana (8%)	Buoyancy (5%)- flagellated (38%)
					Mallomonas multiunca (7%)	Green (24%)- brown (41%)- blue (24%)- mixed (11%)
					Cryptomonas marssonii (5%)	Cell size: 23 (0.6-105)*
					Synedra ulna (4%)	
					Rhizosolenia longiseta (4%)	
					Rhodomonas minuta (4%)	
Parker						
	9.14	0.78	2.54	0.64	*Oscillatoria tenuis* (27%)	Nitrogen fixation (4%)
					Dinobryon sertularia (16%)	Si demand (23%)
					Cryptomonas erosa (11%)	Mixotrophy (38%)
					Microsystis flos-aquae (7%)	Chains/colonies (58%)
					Cyclotella meneghiniana (6%)	Buoyancy (4%)- flagellated (42%)
					Erkenia subaequiciliata (4%)	Green (31%)- brown (35%)- blue (27%)- mixed (8%)
					Mallomonas mangofora (3%)	Cell size: 16 (3.5-82)*
					Ochromonas globosa (3%)	
					Rhodomonas minuta (3%)	
St. Georges						
	4.30	0.82	2.96	0.64	*Anabaena solitaria* (18%)	Nitrogen fixation (5%)
					Golenkinia radiata (12%)	Si demand (24%)
					Cyclotella meneghiniana (7%)	Mixotrophy (22%)

					Chroococcus minutus (7%)	Chains/colonies (57%)
					Pediastrum duplex (6%)	Buoyancy (5%)- flagellated (27%)
					Mallomonas pumilio (5%)	Green (46%)- brown (30%)- blue (19%)- mixed (5%)
					Cryptomonas erosa (5%)	Cell size: 20 (1-150)*
					Crucigenia tetrapedia (4%)	
					Anabaeba flos-aquae (4%)	
					Scenedesmus ecornis (3%)	
					Staurastrum sp. (3%)	
Deep lakes with low FD						
Bowker						
	61.90	0.88	2.39	0.48	*Tabellaria fenestrata* (20%)	Nitrogen fixation (0%)
					Cryptomonas erosa (15%)	Si demand (40%)
					Erkenia subaequiciliata (14%)	Mixotrophy (60%)
					Cyclotella meneghiana (10%)	Chains/colonies (20%)
					Mallomonas mangofera (10%)	Buoyancy (0%)- flagellated (67%)
					Rhodomonas minuta (7%)	Green (20%)- brown (60%)- blue (0%)- mixed (20%)
						Cell size: 28 (4-82)*
Brompton						
	42.4	0.81	2.47	0.56	*Chlamydomonas pseudopertyi* (19%)	Nitrogen fixation (0%)
					Cryptomonas erosa (18%)	Si demand (29%)
					Tabellaria fenestrata (11%)	Mixotrophy (52%)
					Rhodomonas minuta (11%)	Chains/colonies (24%)
					Erkenia subaequiciliata (8%)	Buoyancy (0%)- flagellated (67%)
					Cryptomonas borealis (6%)	Green (33%)- brown (43%)- blue (10%)- mixed (14%)
					Cosmarium depressum (5%)	Cell size: 22 (4-66)*
Lyster						
	42.0	0.86	2.43	0.56	*Asterionella formosa* (21%)	Nitrogen fixation (0%)
					Ochromonas globosa (13%)	Si demand (29%)
					Cyclotella meneghiniana (11%)	Mixotrophy (17%)

					Mallomonas mangofera (11%)	Chains/colonies (47%)
					Golenkinia radiata (9%)	Buoyancy (0%)- flagellated (47%)
					Melosira granulata (6%)	Green (18%)- brown (47%)- blue (18%)- mixed (18%)
					Cryptomonas erosa (6%)	Cell size: 20 (2.5-82)*
Orford						
	39.50	0.69	2.20	0.56	*Ceratium hirundinella* (37%)	Nitrogen fixation (0%)
					Asterionella formosa (15%)	Si demand (25%)
					Rhodomonas minuta (6%)	Mixotrophy (50%)
					Euglena tripteris (6%)	Chains/colonies (46%)
					Mallomonas caudata (5%)	Buoyancy (0%)- flagellated (54%)
					Ochromonas globosa (5%)	Green (25%)- brown (54%)- blue (13%)- mixed (8%)
						Cell size: 17 (1.5-82)*
Silver						
	55.00	0.68	1.89	0.51	*Synura uvella* (42%)	Nitrogen fixation (0%)
					Cryptomonas erosa (18%)	Si demand (19%)
					Chroococcus limneticus (13%)	Mixotrophy (69%)
					Cryptomonas marssonii (9%)	Chains/colonies (25%)
						Buoyancy (0%)- flagellated (69%)
						Green (13%)- brown (44%)- blue (13%)- mixed (31%)
						Cell size: 12 (2-21)*
Laurentians Region						
Shallow lakes with low FD						
Bleu						
	10.70	0.76	2.00	0.52	*Ceratium hirundinella* (32%)	Nitrogen fixation (14%)
					Rhodomonas minuta (19%)	Si demand (7%)
					Cryptomonas erosa (16%)	Mixotrophy (50%)
					Fragillaria crotonensis (11%)	Chains/colonies (57%)
						Buoyancy (7%)- flagellated (50%)
						Green (7%)- brown (43%)- blue (36%)- mixed (14%)
						Cell size: 16 (1.5-63)*

Boeuf						
	10.50	0.75	2.22	0.52	*Uroglena europhaea* (23%) *Golenkinia radiata* (23%) *Cryptomonas erosa* (10%) *Gymnodinium ordinatum* (9%) *Cyclotella meneghiniana* (9%) *Mallomonas caudata* (8%)	Nitrogen fixation (5%) Si demand (16%) Mixotrophy (53%) Chains/colonies (26%) Buoyancy (0%)- flagellated (68%) Green (21%)- brown (53%)- blue (16%)- mixed (11%) Cell size: 10 (1.5-25)*
Cromwell						
	9.90	0.76	2.47	0.47	*Uroglena europhaea* (23%) *Rhodomonas minuta* (20%) *Dinobryon sertularia* (10%) *Oscillatoria agardhi* (9%) *Trachelomonas hispida* (8%) *Crucigenia tetrapedia* (6%)	Nitrogen fixation (0%) Si demand (8%) Mixotrophy (46%) Chains/colonies (58%) Buoyancy (0%)- flagellated (54%) Green (31%)- brown (35%)- blue (27%)- mixed (8%) Cell size: 10 (0.6-40)*
Renaud						
	4.20	0.67	1.86	0.40	*Cyclotella meneghiniana* (34%) *Microsystis flos-aquae* (30%) *Rhodomonas minuta* (11%) *Cryptomonas erosa* (7%)	Nitrogen fixation (0%) Si demand (6%) Mixotrophy (38%) Chains/colonies (44%) Buoyancy (0%)- flagellated (50%) Green (31%)- brown (25%)- blue (25%)- mixed (19%) Cell size: 8 (4-21)*
Deep lakes with high FD						
Achigan						
	26.40	0.79	2.73	0.70	*Pediastrum duplex* (15%) *Cyclotella meneghiniana* (12%) *Dinobryon sertularia* (10%)	Nitrogen fixation (6%) Si demand (26%) Mixotrophy (35%)

				Cryptomonas borealis (10%)	Chains/colonies (42%)
				Anabaena flos-aquae (10%)	Buoyancy (3%)- flagellated (45%)
				Fragillaria crotonensis (9%)	Green (26%)- brown (42%)- blue (19%)- mixed (13%)
				Mallomonas caudata (4%)	Cell size: 20 (1.5-105)*
				Rhodomonas minuta (4%)	
Masson					
45.70	0.83	2.73	0.55	*Chroococcus westii* (26%)	Nitrogen fixation (0%)
				Chlamydomonas vernalis (7%)	Si demand (11%)
				Gomphosphaeria aponina (7%)	Mixotrophy (52%)
				Gomphosphaeria lacustris (6%)	Chains/colonies (44%)
				Cyclotella meneginiana (5%)	Buoyancy (0%)- flagellated (59%)
				Cryptomonas borealis (5%)	Green (15%)- brown (26%)- blue (33%)- mixed (26%)
				Cryptomonas erosa (5%)	Cell size: 11 (1.8-30)*
				Chroococcus limneticus (4%)	
				Merismopedia punctata (4%)	
Montagne-Noir					
33.80	0.78	2.45	0.59	*Cyclotella meneginiana* (21%)	Nitrogen fixation (0%)
				Cryptomonas borealis (17%)	Si demand (35%)
				Cryptomonas erosa (15%)	Mixotrophy (52%)
				Tabellaria fenestrata (10%)	Chains/colonies (39%)
				Uroglena europhaea (8%)	Buoyancy (0%)- flagellated (52%)
				Rhodomonas minuta (6%)	Cell size: 20 (3.5-82)*
Seize-Iles					
59.00	0.71	2.09	0.56	*Fragillaria crotonensis* (33%)	Nitrogen fixation (5%)
				Aphanocapsa pulchra (15%)	Si demand (21%)
				Staurastrum sp. (13%)	Mixotrophy (26%)
				Rhodomonas minuta (10%)	Chains/colonies (53%)
				Asterionella formosa (7%)	Buoyancy (5%)- flagellated (32%)
					Cell size: 19 (2-82)*

*Mean (range) in μm of cell size trait.

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