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Importance relative des producteurs primaires sur la production globale du lac Saint-Pierre, un grand lac fluvial du Saint-Laurent

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Importance relative des producteurs primaires sur la production biologique totale du lac Saint-Pierre, un grand lac fluvial du Saint-Laurent

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SOMMAIRE

Ces dernières années, des fluctuations importantes dans les niveaux d' eau du système des Grands Lacs - Saint-Laurent ont attiré l'attention sur le fait que ces changements pouvaient avoir des impacts écologiques importants dans ces systèmes. Cependant, le manque de données, en particulier sur les communautés situées à la base des réseaux trophiques tels que les producteurs primaires, limite actuellement notre capacité à comprendre le fonctionnement de ces écosystèmes et à prédire leur réponse face à des fluctuations de niveaux d'eau. Cette thèse quantifie, à grande échelle, la production primaire des macrophytes, des épiphytes et du phytoplancton durant deux années avec des niveaux d'eau opposés, dans le Lac Saint-Pierre, un grand (~300 km^2) lac fluvial du fleuve Saint-Laurent.

Une comparaison des méthodes d'estimation de la biomasse et de la distribution des plantes aquatiques émergentes et submergées à l'échelle du lac montre que l'utilisation de modèles empiriques intégrés dans un système d'information géographique (SIG) se révèle efficace pour déterminer la distribution spatiale des macrophytes pour tous les types d'habitats au Lac Saint-Pierre. Une méthode de correction pour les modèles de production primaire phytoplanctonique a été développée pour permettre une application spatiale de ces modèles dans des milieux optiquement complexes tels ceux du fleuve Saint-Laurent. Le taux de photosynthèse des algues épiphytiques est fortement lié à la biomasse algale, et moindrement influencé par la lumière et la température. La distribution de la biomasse des macrophytes et des épiphytes et la réponse photosynthétique en fonction de la profondeur a un effet important sur l'estimation de la production des épiphytes à l'échelle du système. En général, les algues filamenteuses utilisent plus efficacement la lumière que les algues attachées, leur donnant ainsi un avantage compétitif face à des changements de niveau d' eau.

Une analyse de la production primaire totale à l'échelle du lac indique qu'une diminution du niveau d'eau d'un mètre en 2001, comparativement à 2000, a entraîné une réduction de la superficie des marais de 50%, une augmentation dramatique de la production par le phytoplancton dans la zone d'eau libre de 60%, une augmentation de la biomasse et de la production des algues filamenteuses, ainsi qu'une hausse de la production primaire globale de 20%, soit l'équivalent de 5000 tonnes métriques de

carbone. Cependant, la contribution relative des producteurs primaires à l'échelle du lac a été peu affectée par un abaissement du niveau d'eau, en raison de l'hétérogénéité spatiale du système. Une étude spatiale de la production primaire indiquait des variations dans la distribution et dans le type de producteurs entre les années. Cette étude représente la première estimation de la production primaire totale du Lac Saint-Pierre par type de producteur, et l'une des premières estimations quantitatives de production autotrophe totale dans une grande rivière. Les résultats de cette thèse soulignent l'importance d'incorporer l'hétérogénéité spatiale de la production autotrophe pour une vision intégrée du fonctionnement des grandes rivières.

Mots clés: production primaire, rivière, fleuve, SIG, phytoplancton, macrophytes, épiphytes, niveau d'eau

SUMMARY

In recent years, fluctuating flow and water levels in the Great Lakes–St. Lawrence River system have drawn attention to the potential ecological impacts of lower water levels on this system. Total primary production of the St. Lawrence River remains largely unknown, and because primary producers are at the base of the food chain, this lack of information hinders our capacity to understand the flow of carbon and to predict the consequences of altered water levels on ecosystem processes. This thesis examines the primary production of macrophytes, epiphyton and phytoplankton over a 2-year period with contrasting water levels in Lake St. Pierre, a large (~300 km^2) fluvial lake of the St. Lawrence River (Canada).

A comparison of methods used to determine the distribution and biomass of aquatic macrophytes showed that empirical models integrated in a GIS-framework provided the most adequate estimation of macrophyte biomass across the entire range of riverine habitats in Lake St. Pierre. A general model to correct daily phytoplankton primary production estimates for errors arising from variable optical depths was developed to allow for increased spatial and temporal modelling of algal production in diverse, shallow water systems. Epiphyton specific-productivity in Lake St. Pierre was related to biomass, light and temperature and areal estimates of epiphyton production were found to be strongly dependent on vertical variations in light and biomass within macrophyte stands. Filamentous algal mats utilised light more efficiently than attached epiphytes, conferring a competitive advantage over attached forms under conditions of lower water levels.

Analyses of whole-system primary production revealed that macrophytes and epiphyton were responsible for roughly half of annual autotrophic production in Lake St. Pierre. Under low water levels in 2001, coverage by wetted emergent marsh habitats decreased by 50%, phytoplankton production in the open water zone increased by 60%, filamentous algal biomass and production increased dramatically and whole-system carbon production increased by 20 %, or roughly 5000 mt C. Changes in the relative contributions of primary producers to annual production at the scale of the lake between years were relatively minor. Examination of the spatial distribution of production revealed important shifts in the location and type of primary producers. This study

represents the first estimate of primary production and of the relative contributions of the various producing communities in Lake St. Pierre and one of the first quantitative estimates of whole-system primary production in a large river system. Results of this study underline the importance of considering spatial variations in autotrophic production for a comprehensive view of the functioning of large river systems.

Keywords: primary production, large river, GIS, phytoplankton, macrophytes, epiphyton, water level

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À mes parents

"Yes, said the ferryman, it is a very beautiful river...I have oftened listened to it, gazed at it, and I have always learned something from it. One can learn much from a river"

-Hermann Hesse

SIDDHARTHA

"She thought that trying to live life according to any plan you actually work out is like trying to buy ingredients for a recipe from a supermarket. You get one of those trolleys which simply will not go in the direction you push it and end up just having to buy completely different stuff."

-Douglas Adams

MOSTLY HARMLESS

INTRODUCTION GÉNÉRALE

Le rôle de la production primaire dans la structure et le fonctionnement des écosystèmes

La production primaire, ou la conversion de l'énergie solaire en carbone organique par le processus de la photosynthèse, fournit la majorité de l'énergie qui supporte la vie sur terre. La quantité de carbone fixé par les communautés autotrophes ainsi que les facteurs qui influencent cette production sont d'une importance fondamentale pour la compréhension du fonctionnement et de la structure des écosystèmes car elle détermine la capacité de production du système.

Dans les systèmes aquatiques, les producteurs primaires sont représentés par les plantes vasculaires émergentes ou submergées et les algues microscopiques libres dans la colonne d'eau (le phytoplancton) ou attachées à un substrat (le périphyton). Ces groupes sont très variables en terme de diversité, de distribution, de biomasse et de productivité. Implicitement, la contribution relative de chacun des groupes à la production totale du système est variable, et dépend des caractéristiques physiques, chimiques et biologiques du système. (Sand-Jensen & Borum 1991). Un changement de la production primaire et de la contribution relative des plantes vasculaires, des algues benthiques et du phytoplancton a des conséquences sur le flux d'énergie et la dynamique des réseaux trophiques, la structure de l'habitat et le recyclage des nutriments (Wetzel 2001). De nombreuses études démontrent que les algues (phytoplancton et périphyton) sont une importante source de nourriture pour l'ensemble du réseau trophique des systèmes aquatiques d'eau douce (e.g. Cattaneo 1983 en lacs, Hart & Lovvorn 2003 en milieu humides, Feminella & Hawkins 1995 en ruisseau et Thorp et al. 1998 en rivières). Par contre, le carbone fixé par les plantes vasculaires entre principalement dans la chaîne alimentaire sous forme de détritus, lors de leur période de sénescence (Wetzel 2001). Une diminution dans la biomasse et productivité des algues réduit la quantité de nourriture disponible pour les organismes herbivores ce qui conduit en une limitation de la production secondaire pélagique (e.g. Cyr & Pace 1993). A l'inverse, une augmentation de la biomasse et de la productivité des macrophytes favorise le transfert d'énergie vers la chaîne trophique détritique. La composition spécifique des producteurs primaires (espèces de macrophytes, type de communauté algale) peut aussi avoir une

influence sur la composition spécifique des invertébrés (e.g. Hart & Lovvorn 2000) et vice-versa (Hann 1991, Dodds & Gudder 1992). Par exemple, l'étude de Hart & Lovvorn (2000) démontre que, à un niveau de production primaire comparable, un habitat supportant une forte production épiphytique a favorisé les organismes brouteurs et détritivores (Gastropodes et Amphipodes), alors qu'un habitat où la majorité de la production primaire était d'origine phytoplanctonique et benthique a permis le développement d'organismes filtreurs et détritivores (cladocères, copépodes et chironomides).

Un changement dans la composition et la biomasse des plantes vasculaires peut aussi résulter dans des changements chimiques et physiques d'habitats en raison d'une perte de réserve de nutriments et d'un changement dans la configuration physique de l'habitat. Les algues assimilent des nutriments de la colonne d'eau (Wetzel 1990) alors que les macrophytes, par leur système racinaire, puisent la majorité de leurs ressources nutritives dans les sédiments, formant ainsi un lien entre les sédiments et l'eau (Carignan & Kalff 1980, 1982). Les changements saisonniers dans la croissance et la sénescence des macrophytes ont une influence sur le recyclage des nutriments (Carpenter 1980, Carpenter & Lodge 1986). Une forte densité de macrophytes peut aussi influencer le profil vertical d'oxygène, de pH et de lumière dans la zone littorale (e.g. O`Neill Morin & Kimball 1983) et ces gradients influencent à leur tour la disponibilité du carbone et des nutriments pour les autres producteurs primaires et secondaires.

Les macrophytes représentent un habitat important pour les invertébrés, les poissons et la sauvagine. Elles ont aussi un impact sur les propriétés physiques de l'habitat car elles modifient le mouvement de l'eau, absorbent l'énergie des vagues, et filtrent la matière en suspension (Spence 1982). La composition spécifique des macrophytes influence la structure verticale de l'habitat car la forme et l'architecture de la plante déterminent le type de substrat disponible ainsi que les caractéristiques physiques telles que la lumière. Les macrophytes constituent une surface d'attachement pour les algues épiphytiques, ce qui augmente la productivité de ces dernières, en raison de leur position plus élevée dans la colonne d'eau où les conditions de lumière sont souvent plus favorables (Wetzel & Sondergaard 1998). Les plantes submergées offrent plus de surfaces disponibles aux algues que les plantes émergentes car elles s'étendent

horizontalement et verticalement dans l'eau (Cronk & Mitsch 1994) et les différences de biomasse d'épiphytes sont ainsi liées à l'architecture de la plante et à sa densité (Lalonde & Downing 1991, Cattaneo et al. 1998). Les espèces émergentes croissent verticalement dans la colonne d'eau et offrent une surface de colonisation moindre que les espèces submergées (e.g. Grinshaw et al. 1997). Elle peuvent cependant avoir un important effet d'ombrage en surface.

L' importance relative des producteurs primaires dans différents milieux aquatiques

Dans les milieux aquatiques, la contribution relative des producteurs primaires est déterminée en grande partie par la taille du système, sa profondeur et ses concentrations en nutriments (Westlake et al. 1980, Sand-Jensen & Borum 1991). Les grands systèmes profonds, tels que les océans et les grands lacs, tendent à être dominés par la production du phytoplancton. A l'inverse, les lacs peu profonds tendent à être dominés par la production benthique des macrophytes et des algues attachées aux macrophytes ou associées au sédiments. Une forte concentration en nutriments favorise un accroissement du phytoplancton qui réduit la lumière atteignant le fond et diminue la part de la productivité des algues benthiques et des macrophytes (e.g. Sand-Jensen & Borum 1991, Vadeboncoeur et al. 2003). La dynamique des producteurs primaires dans les lacs peu profonds et riches en éléments nutritifs comprend deux états stables, alternant entre un état turbide où le phytoplancton domine et un état d'eau claire où les macrophytes dominent (Philips et al. 1978, Sand-Jensen & Sondergaard 1981, Scheffer et al. 1993). Dans les marais, les plantes vasculaires et les algues benthiques représentent la plus grande part de la production (Goldsborough & Robinson 1996).

En eaux courantes, la répartition des producteurs primaires est moins bien connue qu'en milieu lacustre. En ruisseaux, la production périphytique est prépondérante (Lamberti & Steinman 1997), alors que dans les grandes rivières, le phytoplancton est le principal producteur primaire (e.g. Vannote et al. 1980, Lewis 1988). Cependant, la dominance de la production par le phytoplancton dans les grandes rivières reste en grande partie théorique car peu de données quantitatives existent sur l'importance relative des producteurs primaires dans ce type d'écosystème.

Deux types de modèles théoriques sur le fonctionnement des rivières existent dans la littérature: le premier considère les rivières en terme de gradient physique et biologique longitudinaux (i.e. River Continuum Concept (RCC) Vannote et al. 1980 ou Serial Discontinuity Concept de Ward & Stanford 1983) et le second considère les dimensions latérales (la plaine inondable) et longitudinales (Flood Pulse Concept (FPC) de Junk et al. 1989). Tous ces modèles prétendent que la source majeure d'énergie dans les grandes rivières est le matière organique dérivée des sources terrestres du basin versant, soit en amont (RCC), soit de la plaine inondable (FPC). En contraste, le modèle «Riverine Productivity Model» (RPM, Thorp & Delong 1994) propose que les sources de carbone autochtone que constituent le phytoplancton, les macrophytes et les algues benthiques représentent les principales sources d'énergie supportant le réseau trophique des grandes rivières.

Selon ces théories, l'importance relative des producteurs primaires est variable le long de la rivière et dépend en partie des caractéristiques individuelles de chaque rivière (c.à d. la morphologie et l'hydrologie) (Thorp & Delong 1994, Wetzel & Ward 1996, Naiman et al. 2002). Dans la progression de ruisseau à rivière de moyenne taille, la production autotrophe par le périphyton augmente (e.g. Vannote et al. 1980). Lorsque les rivières de moyenne taille deviennent de grandes rivières, l'augmentation de la profondeur de l'eau et de la turbidité conduisent à un changement dans la communauté des algues, qui, préalablement dominée par des algues attachées, est majoritairement composée de phytoplancton. Cependant, cette progression est influencée par la morphologie individuelle de chaque cours d'eau (Wetzel & Ward 1996). Dans une rivière caractérisée par un canal restreint ayant peu de zone littorale, la production par les macrophytes et les algues benthiques sera négligeable en comparaison à celle des rivières dont la zone littorale (ou plaine inondable) est importante. Dans ce sens, les modèles théoriques sont basés sur des suppositions concernant la morphologie et le régime de débits, et par conséquent, se limitent à une application restreint à ce type de rivière. Néanmoins, la validation de ces modèles est difficilement faisable à cause du manque de méthodes pour déterminer ou estimer la production à grande échelle spatiale (Johnson et al. 1995).

Importance du régime hydrique des grandes rivières

Dans les grandes rivières, le régime de débit exerce une influence majeure sur l'ensemble des caractéristiques physiques, chimiques et biologiques. Le débit de la majorité des grandes rivières est régularisé par des barrages, ce qui altère leur fonctionnement biologique (e.g. Ward & Stanford 1983, Naiman et al. 2002). L'altération du régime de débit dû au réchauffement global est aussi susceptible d'engendrer d'importantes fluctuations saisonnières et inter-annuelles des débits des grandes rivières, avec des conséquences sur la structure et le fonctionnement de ces systèmes (Naiman et al. 2002). L'abaissement du débit et du niveau d'eau coïncide avec une diminution du courant, de la profondeur et du transport de matière en suspension qui, à son tour, influence les composantes biologiques du système. En raison de l'impact écologique potentiel des variations du niveau d'eau, des modèles prédictifs sont nécessaires pour en évaluer les conséquences sur les communautés biologiques.

La majorité des grandes rivières sont riches en éléments nutritifs, et les facteurs physiques tels que la lumière et le courant ont un rôle dominant sur le contrôle de la production primaire des communautés autotrophes. Bien qu'une relation positive entre les nutriments et le phytoplancton ait été démontrée en rivière (Basu & Pick 1996), les facteurs physiques sont plus souvent invoqués pour expliquer la dynamique du phytoplancton en rivière (Reynolds 1988). De plus, les grandes rivières sont souvent soumises à des apports importants de polluants industriels et agricoles provenant du bassin de drainage. Les grandes rivières sont souvent turbides (coefficient d'extinction lumineuse $K > 1\ m^{-1}$) et la quantité de lumière disponible au fond dépend aussi de la profondeur de l'eau (Cole et al. 1991, Reynolds & Descy 1996). Le mouvement unidirectionnel de l'eau représente une contrainte à l'accumulation de la biomasse du phytoplancton qui est constamment déplacé en aval (Reynolds 1988). Cependant, les communautés de macrophytes dans la zone litorale peuvent favoriser le développement du plancton en grandes rivières (Hudon et et al. 1996, Basu et al. 2000). Les courants influencent la distribution et la production des macrophytes et des algues attachées. Quoique des courants modérés puissent avoir un effet positif sur la croissance des plantes en diminuant l'épaisseur de la couche limite, les forts courants ont un effet négatif sur les macrophytes (Spence 1982, Chambers et al. 1991) et le périphyton (McIntire 1966).

Dans les grandes rivières, les facteurs physiques tels que la lumière et le courant sont directement liés au débit et l'altération du régime hydrique peut fortement influencer l'importance relative des producteurs primaires et le fonctionnement biologique des rivières.

Site d'étude

Le fleuve Saint-Laurent (débit annuel moyen à Québec ~12000 $m^3 s^{-1}$) est une des plus grandes rivières d'Amérique du Nord et sa partie eau douce s'étend de la sortie du lac Ontario jusqu'à Trois-Rivières (Québec) situé 600 km en aval. Le long de son parcours, le fleuve alterne entre des corridors étroits (< 4 km) caractérisées par de hautes vitesses de courant (> 0.5 m s^{-1}), et des zones de grands lacs fluviaux caractérisées par de faibles pentes et dans lesquels l'eau circule plus lentement (< 0.5 m s^{-1}). Le débit est régularisé en fonction des demandes en hydroélectricité, de la navigation dans le chenal central (ou Voie Maritime), et en fonction des inondations des rives où il y a des habitations. Récemment, des années de débits et niveaux d'eau très faibles ont permis de mettre en évidence que l'abaissement du niveau de l'eau pourrait induire de graves pertubations écologiques, surtout dans le cas du Lac Saint-Pierre.

Le lac Saint-Pierre est le plus grand (300 km^2) élargissement du fleuve Saint-Laurent situé environ 120 km en aval de Montréal. Le lac représente le plus important herbier du fleuve (~ 120 km^2) et la richesse de sa flore et de sa faune en a fait un site d'importance mondiale classé par RAMSAR et l'UNESCO (http://www.ramsar.org et http://www.unesco.org/mab/). Le lac Saint Pierre est peu profond (profondeur moyenne < 4 m) à l'exception de la voie navigable (>10 m), draguée. En raison de sa faible profondeur et de sa faible pente, ce lac est vulnérable aux changements de niveau d'eau.

Le lac est aussi caractérisé par une forte hétérogénéité spatiale provenant en partie des tributaires qui se déversent en amont et directement dans le lac, formant ainsi des masses d'eau distinctes, qui se mélangent peu (Verrette 1990). La présence de masses d'eau génère une structuration physique et chimique importante, qui influence la biologie. Le long de la rive nord coulent des eaux en provenance des rivières Outaouais, l'Assomption et d'autres petits tributaires. Ces eaux sont colorées (brunes) avec des concentrations de carbone organique dissous (COD) d'environ 5 mg L^{-1} et riches en

nutriments (TP > 30-60 $\mu g\ L^{-1}$, TN ~ 500 $\mu g\ L^{-1}$). Les eaux qui coulent dans le chenal principal et la partie centrale du lac proviennent du lac Ontario. Ces eaux vertes sont transparentes (K ~ 1 m^{-1}), relativement minéralisées (conductivité ~225 $\mu S\ cm^{-1}$), mais aussi relativement riches en éléments nutritifs (TP ~ 20 $\mu g\ L^{-1}$, TN ~ 500 $\mu g\ L^{-1}$). Le long de la rive sud coulent les eaux en provenance des tributaires de la rive sud, notamment des rivières Richelieu, Yamaska et St. François, qui ont un bassin de drainage fortement influencé par les activités agricoles. Les eaux brunes de la rive sud sont donc fortement chargées en matières en suspension, COD (5 - 10 $\mu g\ L^{-1}$), et nutriments (TP ~ 50 $\mu g\ L^{-1}$, TN ~ 700 $\mu g\ L^{-1}$) et sont peu transparentes à la lumière (K ~ 2.5 - 3 m^{-1}). Cette mosaïque spatiale de masse d'eau et de morphologie doit être considérée dans un bilan réaliste de la production primaire à l'échelle du lac.

Objectifs et sommaire des chapitres

L'objectif général de cette thèse est de quantifier la production primaire des macrophytes, du phytoplancton et des algues épiphytiques à grande échelle spatiale afin de déterminer leur importance relative dans le lac Saint-Pierre et de déterminer les effets des variations de niveau d'eau du fleuve sur ces communautés. Pour atteindre ces objectifs, des méthodes visant à quantifier la production primaire à grande échelle ont été développées en utilisant des nouvelles technologies telles que les systèmes d'informations géographiques (SIG) et la télédétection. Les connaissances sur les communautés des macrophytes (Hudon et al. 2000) et du phytoplancton (Blais 2000) dans le fleuve Saint-Laurent, ont servi au développement et à la validation de la modélisation par SIG des communautés du Lac Saint-Pierre (Chapitre 1 et 2). Pour pallier au manque d'information sur les algues attachées, une étude de terrain a été entreprise au lac Saint-Pierre en 2000 et 2001 pour mesurer la biomasse et la productivité de cette communauté. Ces données ont permis de déterminer l'influence des variables environnementales sur la productivité spécifique du périphyton (Chapitre 3) et de développer de modèles prédictifs (Chapitre 4). Finalement, la production totale et la contribution relative des producteurs primaires du Lac Saint-Pierre ont été modélisées à l'aide d'un SIG pour deux années de niveau d'eau très différents (Chapitre 4). *L'hypothèse générale testée est que l'importance relative des communautés des producteurs primaires (macrophytes,*

producteurs primaires (macrophytes, phytoplancton et épiphytes) dans le Lac Saint-Pierre est influencée par la profondeur et la taille du système qui sont en grande partie contrôlés par le régime de débit. Cette hypothèse générale a été évaluée par le biais de quatre hypothèses spécifiques examinant chacune des grandes catégories de producteurs primaires et la somme de leurs contributions.

Le premier chapitre de ma thèse examine l'estimation de la distribution et la biomasse des plantes vasculaires qui se fait en général par des méthodes spatiales telle que la télédétection ou par des modèles empiriques. Cependant, peu d'études ont comparé les résultats de ces différentes méthodes. L'objectif de ce chapitre était de comparer l'efficacité de différents modèles empiriques intégrés dans un SIG afin de prédire la distribution spatiale des communautés de macrophytes dans le Lac St. Pierre. *La première hypothèse spécifique est que les facteurs environnementaux (tels que l'exposition aux vents et vagues, la forme de croissance de la plante, la profondeur de l'eau et la lumière) permettent de déterminer la distribution spatiale de la biomasse maximale des macrophytes émergentes et submergées dans le Lac Saint- Pierre.*

Le deuxième chapitre examine l'utilisation d'un modèle empirique développé en estuaire pour estimer spatialement la production primaire par le phytoplancton dans un grand fleuve. L'objectif était d'estimer la production primaire intégrée sur la colonne d'eau en utilisant un modèle empirique de la littérature en SIG. *La seconde hypothèse spécifique est que la concentration en chlorophylle a, l'éclairement journalier et la profondeur de la zone photique peuvent être utilisés pour prédire la production primaire journalière du phytoplancton intégrée pour toute la colonne d'eau.*

En comparaison avec les macrophytes et le phytoplancton, peu d'études ont examiné la biomasse et productivité des algues attachées dans les grandes rivières. Comme les nutriments sont abondants, la production primaire des épiphytes dans ces systèmes est largement dominée par les conditions lumineuses, le courant et la disponibilité de substrat (biomasse des macrophytes émergentes et submergées). Le troisième chapitre examine la production primaire des algues épiphytiques et filamenteuses dans le Lac Saint-Pierre. L'objectif était de déterminer quels facteurs environnementaux expliquent la plus grande variabilité des taux de photosynthèse des algues attachées. *La troisième hypothèse spécifique est que la productivité épiphytique*

est principalement influencée par les facteurs physiques (tels que la lumière et la disponibilité de substrat).

L'objectif du quatrième chapitre était de quantifier l'importance relative des producteurs primaires à l'échelle du lac et de déterminer l'effet d'une baisse de niveau sur la production totale et l'importance relative des producteurs primaires au Lac Saint-Pierre. Le chapitre utilise l'ensemble des modèles qui ont été développés pour prédire la biomasse ou la production de chaque type de producteur primaire en fonction des facteurs physiques. Par la suite, ces modèles ont été intégrés dans un SIG en combinant des mesures de terrain avec des mesures dérivées de la télédétection pour estimer la contribution relative des producteurs primaires à l'échelle du lac. *La quatrième hypothèse spécifique est qu'une baisse de niveau d'eau engendrera une augmentation de la production primaire autotrophe au Lac Saint-Pierre, en raison d'une augmentation de l'intensité lumineuse moyenne de la colonne d'eau.*

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CHAPITRE 1

An evaluation of approaches used to determine the distribution and biomass of emergent and submerged aquatic macrophytes over large spatial scales

Vis, C., C. Hudon, & R. Carignan. 2003. An evaluation of approaches used to determine the distribution and biomass of emergent and submerged aquatic macrophytes over large spatial scales. *Aquatic Botany* 77: 187-201

Abstract

We compared the performance of various approaches to determine the distribution and biomass of submerged and emergent aquatic plants in a large fluvial lake. Three empirical models linking local macrophyte biomass to single and multiple environmental variables were applied in a GIS-framework to estimate the spatial distribution and biomass of aquatic macrophytes in Lake St. Pierre, a large (300 km^2), shallow (mean depth 3 m) and complex widening of the St. Lawrence River (Quebec, Canada). The resulting maps and emergent and submerged macrophyte distributions obtained independently by remote sensing and echo sounding techniques were compared to field data collected in 2000. Maps derived from echo sounding, from a biomass versus depth regression and from a four-variable model (i.e. exposure to wind and waves, plant growth form, water depth and transparency) were the most accurate (55-63% overall agreement with field data). Remote sensing techniques were the least accurate for determining underwater macrophyte distribution in Lake St. Pierre due to the limitations of image-based methods for detecting submerged aquatic vegetation in coloured, turbid waters. This study demonstrates that environmental models in combination with GIS can be used to estimate aquatic macrophyte distribution over larger spatial scales and to examine potential change in macrophyte growth form assemblages arising from different environmental conditions.

Keywords: Macrophytes; GIS; Remote sensing; Echo sounding; St. Lawrence River; Growth form.

Introduction

Information on the areal biomass and distribution of aquatic vegetation are necessary for the monitoring, management and understanding of shallow aquatic ecosystems. Determining macrophyte cover and biomass is difficult, however, both at small and large spatial scales because of the spatial heterogeneity of these communities (Downing and Anderson, 1985; Duarte and Kalff, 1990a). Several approaches have been used to determine the distribution and biomass of emergent and submerged vegetation at various spatial scales, including direct field measurements, indirect

mapping methods such as remote sensing, and various modelling methods; however, they have been subject to little cross validation.

Traditional methods for studying aquatic macrophytes are based on direct field observations and measurements within quadrats or along transects. These methods are labour intensive and for this reason, only applicable to small areas. Such studies have, however, identified the main environmental factors influencing the distribution of macrophytes and have led to the development of several empirical relationships which predict macrophyte biomass from environmental variables such as slope (Duarte and Kalff, 1986), current velocity (Chambers et al., 1991) or fetch (Chambers, 1987). Geographic Information Systems (GIS) can be used to translate these relationships into spatially explicit representations of macrophyte distributions over broad areas (i.e. Lehmann, 1998; Lathrop et al., 2001).

Airborne and satellite imagery, video and echo sounding techniques have been used to map the distribution of aquatic vegetation over various spatial scales in marine, estuarine and freshwater environments (Lehmann and Lachavanne, 1997). These techniques provide a synoptic view of an entire system, but are limited by image quality, water depth, stage of plant growth, turbidity and wind (Orth and Moore, 1983; Duarte, 1987). These techniques require field surveys to provide accurate interpretation of image or tracing data, and vegetation is usually grouped into broad categories from which presence/absence or percent cover data is estimated.

Here, we use field data to assess the performance of remote sensing, echo sounder data and three environmental models applied in a GIS-framework to predict the distribution of emergent and submerged macrophytes in a large fluvial lake (300 km^2). We then compare these techniques to determine the most efficient method in view of their respective limitations.

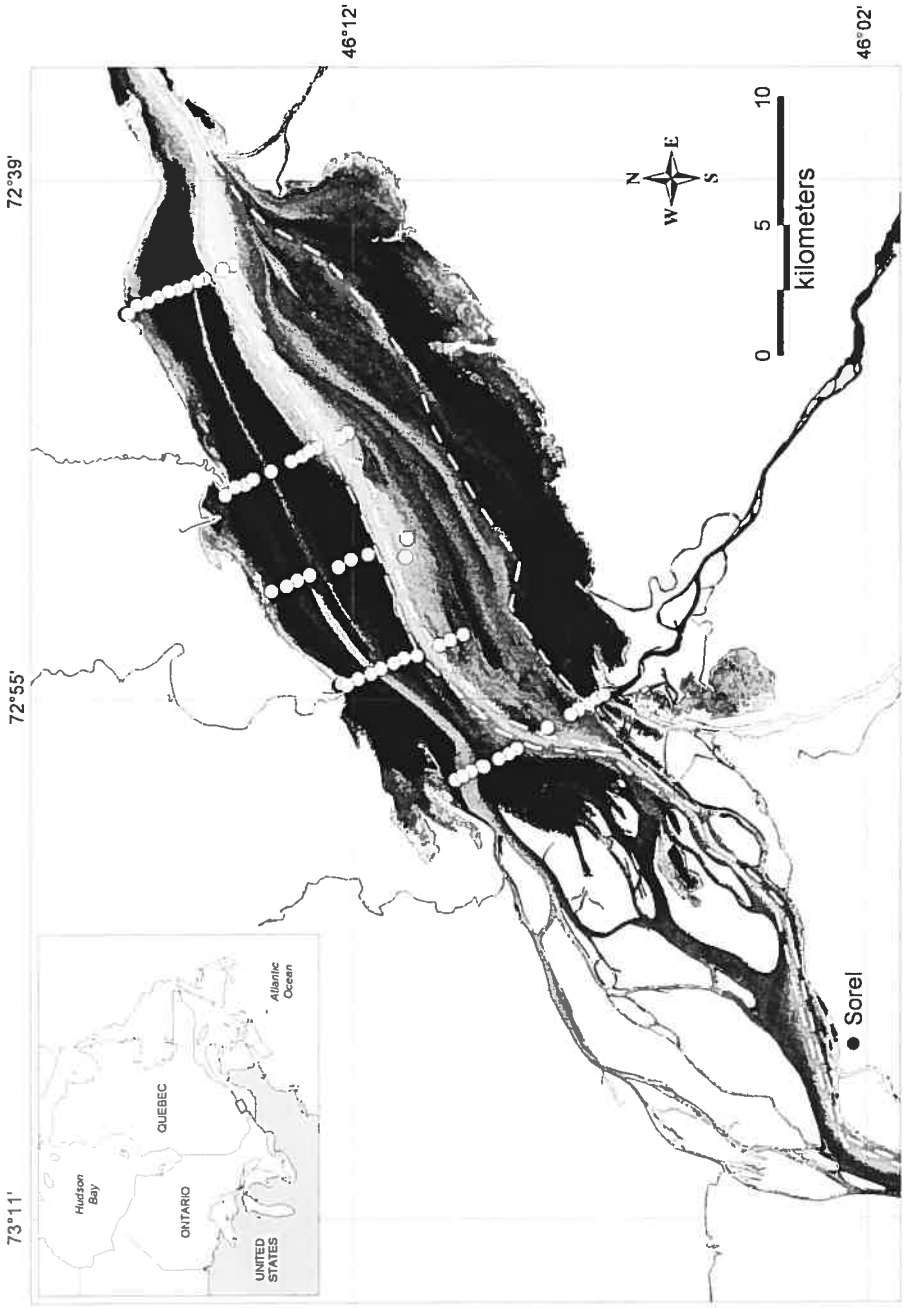
Study area

Lake St. Pierre, the largest fluvial lake (300 km^2) of the St. Lawrence River, is an environmentally complex system, where factors known to influence the distribution of macrophytes (such as water depth, light and current) vary over tens of kilometres (Fig. 1). The lake is shallow (< 4 m) over most of its surface, with the exception of the deep

(> 11.3 m) navigation channel that bisects the lake (Fig. 1; Table 1). The shallow waters and gently sloping shores have favoured the development of large expanses of submerged and emergent aquatic vegetation. Approximately 20% of the St. Lawrence River wetlands are found within Lake Saint-Pierre, providing habitat for a productive and diverse fauna (Langlois et al., 1992). Submerged vegetation is dominated by *Vallisneria americana* Michx., *Potamogeton Richardsonii* (A. Bennett) Rydb. and *Stuckenia pectinata* (L.) Börner. Large marshes colonized by species of *Schoenoplectus lacustris* (L.) Pallu, *Typha angustifolia* L., *Sagittaria latifolia* Willd. and *Sparganium eurycarpum* Engelm. are especially widespread in the sheltered bays of the south shore and on the downstream side of islands.

Part of the complexity of the lake is due to the presence of distinct water masses originating from various tributaries flowing into the St. Lawrence River (Fig. 1). Mean annual discharge (1973-1998) in Lake St. Pierre is approximately 11 500 m^3 s (Bouchard and Morin, 2000). Waters of the Ottawa River and other tributaries draining the Precambrian Shield flow along the north shore of Lake St. Pierre and represent 13% of the mean annual discharge in Lake St. Pierre. These waters have a low conductivity, a relatively high total phosphorus concentration, and a high DOC concentration which gives them a characteristic brown colour (Table 1). Waters originating from Lake Ontario predominate in the lake in terms of flow (80% of discharge), but are restricted to the central navigation channel and adjacent southern shallow area; these waters are more mineralised, poorer in total phosphorus and less turbid than those flowing close to the shores. Tributaries draining farmlands on the south shore of the St. Lawrence (Richelieu, Yamaska and Saint-François rivers) bring turbid, brown and nutrient-rich waters along the south shore of Lake St. Pierre (Table 1). This large system therefore presents a diverse combination of physical and chemical characteristics which are expected to influence the distribution and biomass of macrophytes over large spatial scales (Holling, 1992).

Figure 1. Map of Lake St. Pierre, St. Lawrence River, its major tributaries and the distribution of its water masses. The location of the field survey sites (circles) and the boundaries of each water mass (hatched white lines) are indicated on a black and white satellite image (Landsat TM from September 16, 1988). The water masses are from north to south: the north shore, the navigation channel, the central area and the south shore.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Hudson Bay
QUEBEC
ONTARIO
UNITED STATES
Atlantic Ocean

Table 1. Physical, chemical and biological characteristics (mean ± 1 S.E.) of the different water masses in Lake St.Pierre.

	Water mass			
	North shore	**Navigation Channel**	**Central area**	**South shore**
Major Influence	Ottawa River and north shore tributaries	Lake Ontario	Lake Ontario	Richelieu, Yamaska and St.François rivers
Mean annual flow ($m^3 s^{-1}$)	1500	9300		700
Surface area (km^2)	124	17	86	78
Average depth (m)	3.0	11.6	3.8	1.4
Total phosphorus[a] ($\mu g L^{-1}$)	55 ± 11	30 ± 2	22 ± 1	53 ± 3
Total nitrogen[a] ($\mu g L^{-1}$)	566 ± 74	439 ± 19	488 ± 70	613 ± 54
DOC[a] ($mg L^{-1}$)	4.9 ± 0.2	3.1 ± 0.1	2.6 ± 0.1	5.5 ± 0.3
Conductivity[b] ($\mu S cm^{-1}$)	192 ± 3	245 ± 4	257 ± 3	203 ± 8
pH[b]	7.63 ± 0.03	7.88 ± 0.04	8.02 ± 0.06	7.67 ± 0.06
Current speed[b] ($m s^{-1}$)	0.22 ± 0.01	0.65 ± 0.08	0.19 ± 0.02	0.25 ± 0.04
Light extinction coefficient[b] (m^{-1})	1.53 ± 0.04	1.05 ± 0.04	1.01 ± 0.04	2.52 ± 0.26
Chl.a[b] ($\mu g l^{-1}$)	2.45 ± 0.11	1.70 ± 0.14	2.07 ± 0.16	10.14 ± 1.61

[a] C. Hudon, unpublished data (June – Sept. 2000)
[b] C. Vis, unpublished data (May – Oct. 2000)

Methods

We compared five techniques used to map the biomass and/or species assemblage of aquatic macrophytes which were either previously published as maps (remote sensing map by Létourneau and Jean, 1996 and echo sounder tracings map by Fortin et al., 1993) or as non-spatial environmental models (Hudon, 1997; Hudon et al., 2000) with field data collected in 2000. For the maps, we briefly summarise the methods used and readers should refer to the original sources for detailed descriptions.

For the three environmental models which predict average maximum aboveground biomass of both emergent and submerged macrophytes on the basis of one or several environmental factors, we detail only the methods used to integrate these models into a GIS to generate spatially explicit maps of maximum dry aboveground macrophyte biomass.

Remote sensing

To determine land-use and the distribution of vegetation in the St. Lawrence River, airborne Multispectral Electro optical Imaging Scanner (MEIS-II) images (26 July 1990 and 21 August 1990) were classified using supervised pixel-by-pixel classification methods (maximum likelihood methods) based on training sets derived from existing maps and field surveys (Létourneau and Jean, 1996). Fourteen vegetation categories were present in Lake St. Pierre. The classified raster image (provided by G. Létourneau, St. Lawrence Centre, Environment Canada, 105 McGill Street, 7th floor, Montréal, QC, H2Y 2E7, personal communication) had a resolution of 7 x 7 m which was resampled to a pixel size of 21 x 21 m, the areal unit of analysis of the present study.

Echo sounding

Broad classes of submerged aquatic vegetation (by dominant species and relative density) were mapped by Fortin et al. (1993) from echo sounder tracings obtained along 23 georeferenced transects spaced one kilometre apart between August 25 and September 6, 1990. In combination with a field survey, tracings were classified into vegetation categories on the basis of plant architecture determined by the dominant growth form in the stand and of relative density determined by the continuous or discontinuous cover of vegetation along each transect. Vegetation categories were interpolated between transects to produce a distribution and cover map of submerged vegetation for the zone surveyed (hereafter referred to as the deep water zone). Measurements of aboveground biomass of submerged vegetation (g dry mass m^{-2}) made during the field survey were used to assign a mean biomass value to each category of submerged vegetation (St-Cyr et al., 1992). A hard copy of the original map (provided

by G. Fortin, Bureau d'audience publiques sur l'environnement, Édifice Lomer-Gouin, 575 rue Saint-Amable, bureau 2.10, Québec, QC, G1R 6A6, personal communication) was digitized and converted to a 21 x 21 m pixel size grid.

Mapping of environmental models

The first model or discrete depth model associates a mean maximum aboveground biomass to each discrete one metre depth interval between 0 and 5 m (Hudon, 1997). To map this model, we classified a bathymetric map of Lake St. Pierre adjusted to the average water level of 1990 (Chart Datum reference level (CD + 1 m)) into one metre depth intervals and assigned pixels within each interval with the corresponding mean biomass value: 629 g m^{-2} (0-1 m), 266 g m^{-2} (1-2 m), 166 g m^{-2} (2-3 m), 124 g m^{-2} (3-4 m) and 103 g m^{-2} (4-5 m). All pixels with depths greater than five metres were assigned a biomass value of zero.

The continuous depth model uses a biomass versus depth regression to predict maximum aboveground macrophyte biomass (B in kg m^{-2}) from the following polynomial equation:

$$\log_{10} B = -0.65 - 0.75 \log_{10} Z - 0.23 (\log_{10} Z)^2 , r^2=0.31, N=252 \qquad (1)$$

where Z is the water depth (m) (Hudon, 1997; Hudon et al., 2000). Equation 1 was applied to the bathymetric map (value of Z for each pixel) to map this model. All pixels with depths greater than five metres were considered to be devoid of vegetation and assigned a biomass value of 0 g m^{-2}.

A third model, termed the four-variable model, is a hierarchical analysis which predicts aboveground macrophyte biomass (emergent and submerged) on the basis of a combination of four variables: exposure to wind and waves (sheltered, exposed), plant growth form (canopy, non-canopy), water depth (in metres) and transparency (percentage of surface light reaching the bottom) (Hudon et al., 2000). Each of the four environmental variables was mapped and represented layers of information which were combined using Boolean operations in a GIS to generate a composite map of macrophyte biomass. Exposure to wind and waves was mapped by considering all

pixels within the continuous limit of emergent vegetation as sheltered, and those outside the limit as exposed. The limit of emergent vegetation in late summer 2000 was determined by a field survey. Plant growth form was a variable describing whether or not macrophytes reached the surface and thereby formed a canopy. Although direct measurements of this variable for the entire area of Lake St. Pierre were not made, previous studies in the St. Lawrence River have found that, in general, plants growing at depths of less than two metres may reach the surface (Hudon et al., 2000). This variable was mapped as a binary variable by classifying the bathymetric map into depths of greater than (non canopy) and less than two metres (canopy-forming). Transparency, measured as the percentage of light reaching the bottom, was calculated over the entire surface of Lake St. Pierre using the light extinction coefficients of each water mass (Table 1), the mean distribution of water masses and the bathymetric map. A map of bottom light intensity was then classified into two maps with binary values of greater than and less than 20 and 40% light, respectively, which represented the thresholds distinguishing various macrophyte groups in the hierarchical analysis of Hudon et al. (2000). The mean distribution of the water masses was delineated from ten Landsat MSS and TM satellite images taken during the growing season between 1973 and 1990 for which water levels were approximately one metre over navigation charts or Chart Datum reference (mean = 1.00, S.D. = 0.22, n = 10). These layers of information along with the bathymetric map were combined using Boolean queries to construct the composite map of biomass predicted by the four-variable model.

Field data

To assess the accuracy of each method in predicting the distribution of macrophytes, we conducted a field survey in Lake St. Pierre in the summer of 2000. Macrophyte biomass and species composition were sampled during July and August (period of maximum macrophyte biomass) at 77 points located along five transects (Fig. 1). Four of the five transects did not extend over the entire lake because access to the southern section is prohibited by the Department of National Defence of Canada. At each sampling point, SCUBA divers collected three to five replicate samples of all macrophytes growing within a 25 x 25 cm quadrat. In the laboratory, samples were

cleaned of epiphytes and sediments, identified to species, dried (60°C for 24 hours) and weighed.

Effects of inter-annual differences in water level and clarity

Inter-annual differences in water level/depth and clarity were accounted for in the comparison between maps produced by remote sensing and echo sounding both determined in 1990 with predictions from environmental models (developed from data acquired during 1993, 1994 and 1996) and with field data (acquired in 2000). We computed mean values of water levels and suspended matter concentrations over the growing season (June 1 to September 30) for all years studied. Daily water level data for Lake St. Pierre, adjusted to Chart Datum reference levels, was obtained from the Marine Environmental Data Services (Fisheries and Oceans Canada) for the 1990-2000 period (gauging station Curve No. 2 or 02OC016). Daily suspended matter concentrations for a station located near Quebec City (160 km downstream) were obtained from Pierre Gagnon (St. Lawrence Centre, Environment Canada, 105 McGill Street, 7th floor, Montréal, QC, H2Y 2E7, personal communication). Suspended matter concentrations were used because turbidity or light extinction data were not available for all years and there exists a linear relationship between suspended matter and light extinction in the St. Lawrence River (Hudon and Sylvestre, 1998).

Accuracy assessment

Remote sensing and echo sounding surveys produce maps of broad categories of wetland and submerged vegetation, whereas empirical methods map biomass (g m^{-2}) directly. To compare the performance of the various methods, submerged and emergent macrophytes were grouped into growth form/functional groups on the basis of biomass, species composition and plant morphology. These growth form groups were chosen to be representative of the major distinctions in wetland habitat structure and function (Table 2). In deep water, submerged vegetation are limited by light transparency (i.e. Middlebøe and Markager, 1997) and current velocity (i.e. Chambers et al., 1991), resulting in areas devoid of vegetation or areas with low macrophyte biomass dominated by rosette-type vegetation such as *V. americana* Michx. with tapered leaves adapted to flow (groups 1 and 2, respectively). In shallow water areas, low flow and more

favourable light conditions foster the vertical expansion of submerged vegetation in the entire water column (group 3). These areas tend to be dominated by structurally diverse species such as *Myriophyllum* L. and provide important habitat for macroinvertebrates and fish (i.e. Cyr and Downing, 1988). In the very shallow areas, the transition between emergent and submerged vegetation is characterised by a high density of submerged plants interspersed with emergent vegetation (group 4) grading into areas dominated solely by emergent vegetation (group 5). These areas are characterised by a high biomass of robust vegetation and provide important habitats for fish and waterfowl (Weller, 1978; Crowder and Bristow, 1988). Maps were grouped into these broad growth form assemblages on the basis of species composition (remote sensing), biomass (discrete and continuous depth models) or both (echo sounding, four-variable model and field data).

We calculated various measures of accuracy between field data and predicted data for each method at each corresponding location (pixel), including overall accuracy, the Kappa statistic and Producer and Consumer's accuracy (Congalton, 1991). Overall accuracy is calculated as the percent agreement (sum of pixels with same group / total number of pixels). The Kappa statistic (κ) is a coefficient of agreement which tests whether the agreement between 2 judges rating the same object (the diagonal counts of the contingency table or percent agreement) is larger than expected by chance alone. Producer's accuracy is calculated as the total number of correctly classified pixels for a group divided by the total number of observed pixels for that group and indicates how well field data were classified. Consumer's accuracy is calculated as the total number of correctly classified pixels for a group divided by the total number of predicted pixels for that group and indicates the probability that a classified pixel actually represents that category in the field.

All digitising of vector-based maps and delimitation of water masses from Landsat MSS and TM satellite images were done using MapInfo Professional v.6.5 and all raster-based analyses were performed with ARC/INFO GIS v.7.2.1 and ArcView GIS v.3.1.

Table 2. Summary of the macrophyte growth form groups used in the comparison among methods.

Group	Description	Aboveground dry biomass ($g\ m^{-2}$)	Major species
1	No vegetation	0	
2	Non canopy-forming submerged macrophytes	< 150	*Vallisneria americana* Michx., *Heteranthera dubia* (Jacq.) MacM., *Chara* spp. Valliant
3	Canopy-forming submerged macrophytes	150 – 250	*Potamogeton Richardsonii* (A. Bennett) Rydb., *Stuckenia. pectinatus* (L.) Börner, *Myriophyllum* spp. L. , *Elodea canadensis* Michx., *Vallisneria americana* Michx., *Heteranthera dubia* (Jacq.) MacM., *Chara* spp. Valliant
4	Transition zone – submerged and floating-leaved vegetation interspersed among emergent vegetation	250 – 500	*Elodea canadensis* Michx., *Myriophyllum* spp. L. , *Ceratophyllum demersum* L., *Vallisneria americana* Michx., *Lemna minor* L., *Nuphar variegata* Durand, filamentous algae
5	Emergent macrophytes	> 500	*Schoenoplectus lacustris* (L.) Pallu, *Bolboschoenus fluviatilis* (Torrey) S. Sojak, *Typha angustifolia* L., *Sagittaria latifolia* Willd, *Sparganium eurycarpum* Engelm., *Phalaris arundinacea* L., *Spartina pectinata* Link, *Lythrum salicaria* L.

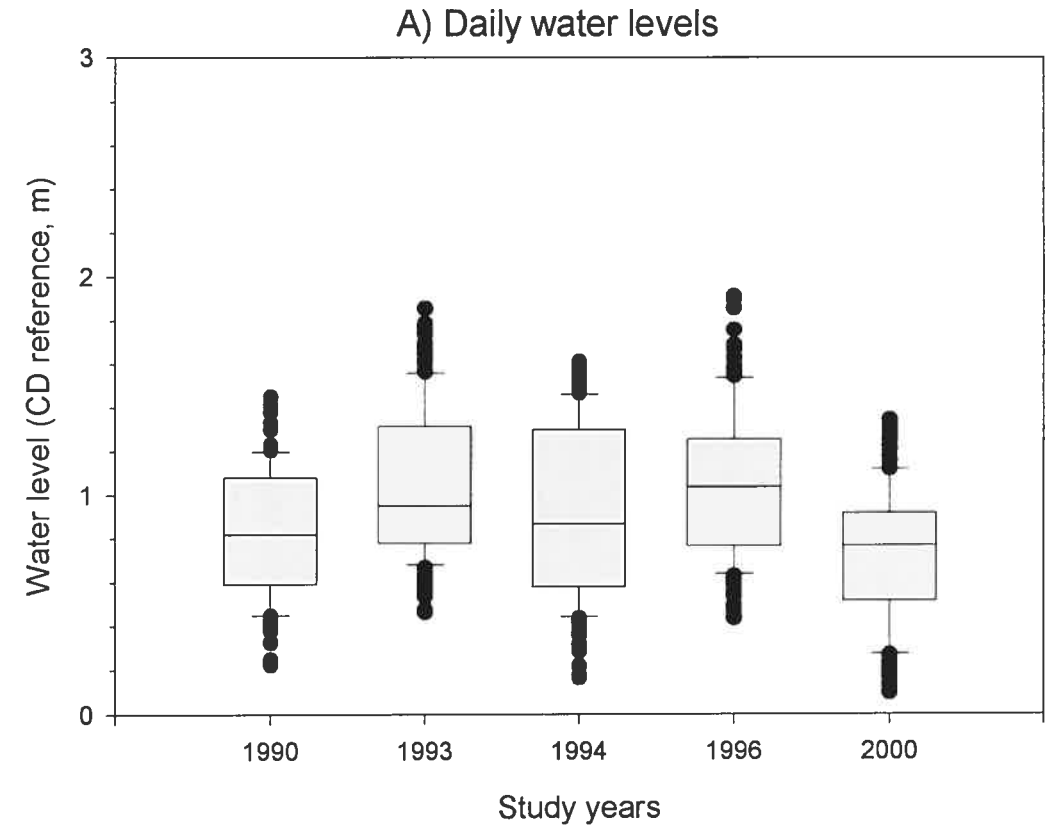
Results

Short-term fluctuations in daily water level and suspended matter concentration within a growing season were large, with a range in daily water level of 0.2 to 1.9 m and in suspended matter of 4.9 to 56.4 mg L^{-1}. Average water levels (mean 0.96 m) and suspended matter concentrations (mean 13.0 mg L^{-1}) were however similar, indicating no major differences in water levels or light conditions between years (Fig.2). Visual examination of the distribution of macrophyte growth form groups predicted by the five methods showed similar patterns of vegetation distribution with emergent and dense submerged macrophytes present in the shallow water zones and submerged non canopy-forming vegetation covering the majority of the surface of the lake (Fig. 3). Remote sensing did not detect the presence of non canopy-forming submerged vegetation and was the least accurate method, having low overall agreement with field data (18%), low Consumer's accuracy and a negative κ value, indicating less observed agreement than expected by chance alone. Echo sounding, the continuous depth and the four-variable models were the most accurate techniques for predicting macrophyte growth form group in Lake St. Pierre (63, 62 and 54 % overall agreement with field data, respectively; Table 3). Echo sounding demonstrated relatively good accuracy in classifying non canopy-forming submerged and no vegetation areas (59-73% Consumer's accuracy). The continuous depth and the four-variable model had low Producer's accuracy for areas devoid of vegetation, tending to predict the presence of submerged non-canopy forming plants (group 2) where none were present. The discrete depth model performed poorly, showing <30% overall accuracy with field data. The assessment of the accuracy of techniques to predict the shallow water groups (groups three to five) was limited because of the low number of reference pixels located within this zone (less than ten)

Discussion

Empirical relationships established between macrophytes and environmental factors can be applied to large areas when spatially explicit environmental data are available. However, fine scale heterogeneity or spatial patchiness in the distribution of macrophytes is difficult to predict using environmental models. For example,

Figure 2. Box plots of (A) Daily water levels and (B) Suspended matter concentrations for the years compared in the study (1990, 1993, 1994, 1996, 2000).


A) Daily water levels
Water level (CD reference, m)
0
1
2
3
1990
1993
1994
1996
2000
Study years

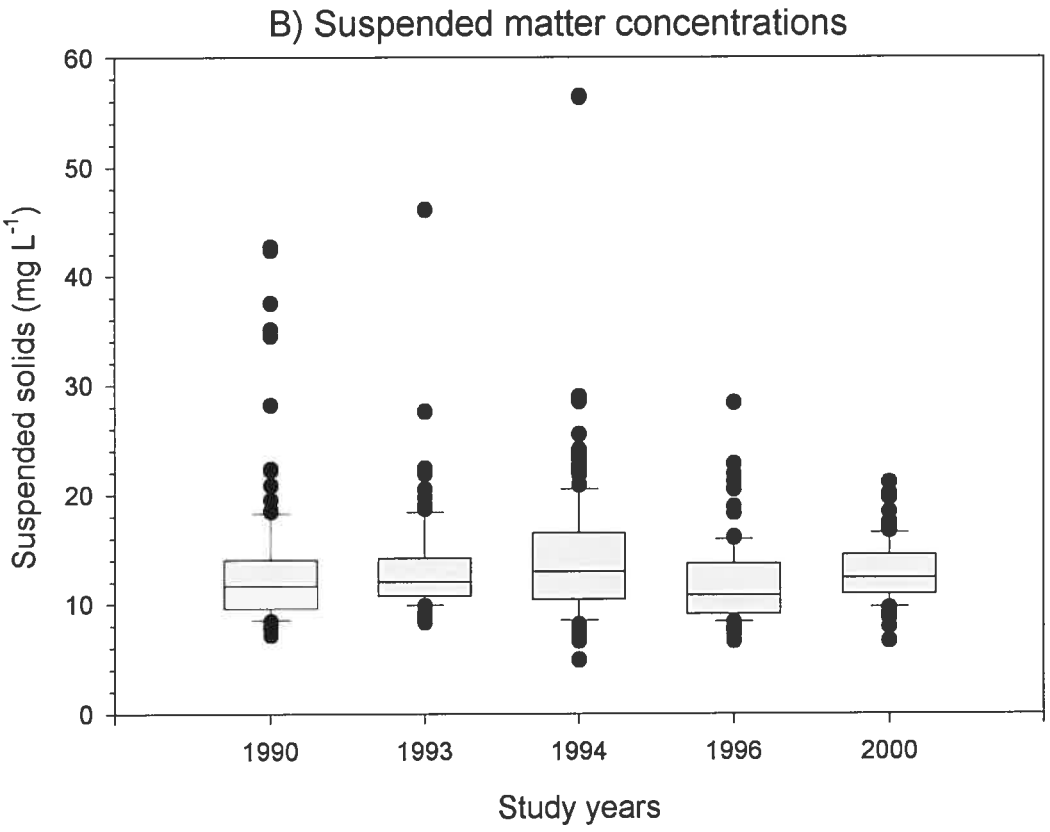

B) Suspended matter concentrations
Suspended solids (mg L-1)
0
10
20
30
40
50
60
1990
1993
1994
1996
2000
Study years

Figure 3. Distribution of macrophyte growth form groups estimated by five methods (A-E) and map of the field data for Lake St. Pierre. Areas compared in this study are indicated on the remote sensing and field data map (solid line: CD + 1m water limit and dotted line: deep water zone). Thatched area not surveyed by echo sounding.

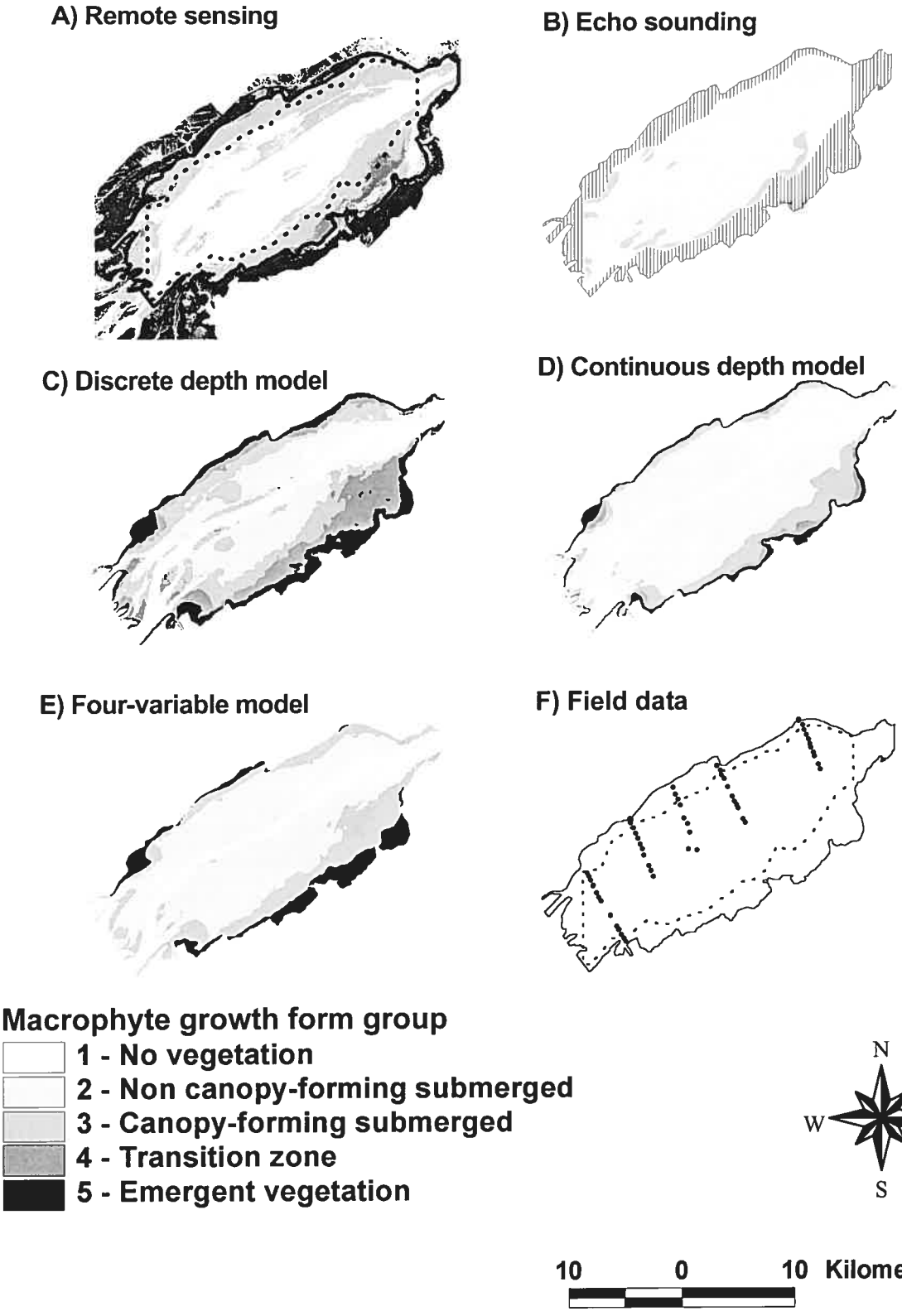

A) Remote sensing
B) Echo sounding
C) Discrete depth model
D) Continuous depth model
E) Four-variable model
F) Field data
Macrophyte growth form group
1 - No vegetation
2 - Non canopy-forming submerged
3 - Canopy-forming submerged
4 - Transition zone
5 - Emergent vegetation
N
W
E
S
10 0 10 Kilometers

Table 3. Accuracy of predicted occurrence of macrophyte growth form groups (group 1-5) for each method. The observed total is the number of field data pixels for each macrophyte growth form group, the predicted total is the number of predicted pixels for each group and the correct total is the number of correctly classified pixels for each group. Four measurements of accuracy are used: Percent agreement, Kappa statistic κ, Producer's and Consumer's accuracy. (see Methods for more information).

Method	Group	Observed total [O]	Predicted total [P]	Correct Total [C]	Producer's accuracy (%) [C]/[O]	Consumer's accuracy (%) [C]/[P]
Remote	1	23	46	12	52	26
sensing	2	38	0	0	0	-
	3	2	25	0	0	0
	4	6	3	1	16	33
	5	5	0	0	0	-
	total	74	74	13	**Overall = 18**	**κ = -4**
Echo	1	19	17	10	53	59
sounding	2	31	30	22	71	73
	3	1	4	0	0	0
	total	51	51	32	**Overall = 63**	**κ = 28**
Discrete	1	23	2	2	9	100
depth	2	37	24	14	38	58
model	3	1	23	0	0	0
	4	1	11	0	0	0
	5	4	6	4	100	67
	total	66	66	20	**Overall = 30**	**κ = 10**
Continuous	1	23	3	3	13	100
depth	2	37	51	33	89	65
model	3	1	7	0	0	0
	4	1	1	1	100	100
	5	4	4	4	100	100
	total	66	66	41	**Overall = 62**	**κ = 31**
Four-	1	23	3	3	13	100
variable	2	37	46	29	78.	63
model	3	1	12	0	0	0
	4	1	0	0	0	-
	5	4	5	4	100	80.0
	total	66	66	36	**Overall = 54**	**κ = 22**

environmental models based on water depth did not predict the absence of submerged vegetation in two large channels (Fig. 3B) maintained vegetation-free by strong currents (Fortin et al., 1993). Despite such limitations, environmental models provide an estimate of the area covered by each macrophyte growth form assemblage which can be used to model large-scale effects of environmental changes.

Differences in the distribution of macrophyte growth form groups between methods are not the result of major differences in water levels or water clarity between study years. Despite large short-term fluctuations in water levels and suspended matter concentrations within each year, the average conditions during the growing season did not change dramatically among years (less than 30 cm in the case of water level and less than 1.2 g L^{-1} for suspended matter).

The general agreement between the three environmental models is not surprising given the importance of water depth in determining the zonation of aquatic plants and in structuring aquatic macrophyte communities (i.e. Remillard and Welch, 1993; Lehmann, 1998). The expression of the relationship between water depth and macrophyte biomass did, however, influence the accuracy of the prediction. Macrophyte growth form assemblages in Lake St. Pierre were most accurately predicted as a continuous function of water depth and the discrete depth model showed poor agreement with field data. The biologically more realistic four-variable model, which included the influence of exposure, transparency, plant growth form and water depth also had a lower accuracy than the continuous depth model. Other studies have also found that although more complex models may present a better fit with observed data and be more realistic, predictions based on these models can be less accurate (i.e. Ludwig and Walters, 1985).

While remote sensing is one of the most widely used methods for determining the large-scale distribution of aquatic vegetation in numerous environments (Lehmann and Lachavanne, 1997), we found it to be the least accurate method in Lake St. Pierre due to the masking effects of water colour and turbidity. As remote sensing is best suited to the identification of emergent vegetation (marshes, meadows and swamps), further study is required to properly assess the performance of this technique for the floodplain area, which was excluded from the present study.

Environmental models were the only methods that provided quantitative estimates of aquatic plant assemblages for the entire area of the lake, and in particular within the transition zone between emergent and submerged vegetation. In aquatic systems in general, but particularly in rivers with large floodplains, the boundary between various classes of emergent, floating-leafed and submerged vegetation is not distinct, as these communities merge into one another along the slope from terrestrial to pelagic zone. Although echo sounding performed well in comparison to field data in estimating submerged vegetation cover in Lake St. Pierre, this method is limited to water depths greater than 70 cm (Duarte, 1987) and is problematic under dense canopy conditions (Fortin et al., 1993; Sabol et al., 2002), rendering echo sounding surveys incompatible with monitoring of macrophytes within the transition zone. In the case of Lake St. Pierre, this shallow water zone contributed ~ 60% of the total aboveground plant biomass, is an area of ecological importance to many organisms, and will be the area most affected by changing water levels (Hudon, 1997).

Image-based methods, such as remote sensing, are expensive and problematic under unfavourable meteorological conditions. Although less expensive, echo sounding requires field sampling surveys and the effort required for the interpretation of tracing data for large systems is not negligible. In both cases, field surveys are required to interpret the image or tracing. In the case of monitoring studies, new images or tracings must be acquired and analysed when environmental variables have changed.

Biomass, plant morphology (growth form) and species composition are inter-related in macrophyte communities (Duarte and Kalff, 1990b; Hudon et al. 2000), and macrophyte growth form groups are strongly related to the ecological function of macrophytes in aquatic systems. Emergent macrophyte communities are characterised by high productivity and their dense canopies shade understory vegetation. These regions provide habitat for waterfowl and mammals (Weller, 1978; Crowder and Bristow, 1988). In shallow zones, submerged aquatic vegetation reaching the surface form structurally diverse habitats used by invertebrates, fish and epiphytic algae (Mitsch and Gosselink, 1993). Submerged vegetation in deeper water can influence flow and flow-related factors such as water velocity and level in large river systems (Boudreau et al., 1994; French and Chambers, 1997). As a result, an environmental model approach

predicting major assemblages of macrophyte growth form is useful for both managers and ecologists. Overall, models based on direct field measurements of multiple environmental variables provide the most complete, effective estimation of macrophyte biomass across the entire range of wetland habitats.

Acknowledgements

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CHAPITRE 2

Estimating daily phytoplankton production in shallow water systems: correcting for variable optical depths

Vis, C., A.-M. Blais & R. Carignan. Estimating daily phytoplankton production in shallow water systems: correcting for variable optical depths. *Ecological Modelling*. Submitted.

Abstract

The theoretical euphotic depth (1% surface irradiance) of many shallow water ecosystems often exceeds actual depth. In such systems, estimates of areal phytoplankton production using empirical models developed for optically deep systems will overestimate production. Here, we present a general model which corrects estimates from daily phytoplankton primary production models for errors arising from variable optical depths, applicable to both optically deep and shallow environments. Based on phytoplankton productivity data from the St. Lawrence River, the relationship between integrated areal production ($P_{Z,t}$) and the product of water depth (Z) and light attenuation (K) was fit to a generalised von Bertalanffy growth equation, with the asymptote of the relationship equal to production integrated over the entire euphotic depth. As an example of the use of the model, we compared estimates of primary production in Lake St. Pierre, a large fluvial lake of the St. Lawrence River, uncorrected and corrected for variable optical depths. Daily primary production was estimated using a modified composite parameter $BZ_{eu}I_oT$ which estimates production from biomass (B or Chl *a*), euphotic zone depth (Z_{eu}), daily irradiance (I_o) and water temperature (T), and explained 85% of the variation in euphotic zone primary production in the St. Lawrence River. Depth corrections to whole-lake areal production averaged 22 %, and corrections in some shallow locations were >95%. The model presented here is easily integrated into a geographic information system (GIS) to generate phytoplankton primary production maps in optically complex ecosystems.

Keywords: Phytoplankton; primary production; large rivers; estuaries; GIS; optical depth

Introduction

Phytoplankton primary production is usually estimated from the relationship between photosynthesis and irradiance (P-I curve) where P is measured either as carbon uptake (^{14}C) or oxygen evolution rates during incubation under a range of light conditions. Models of varying complexity are then used to integrate the P-I curve over time and depth, using light attenuation in the water column and surface irradiance data to

calculate daily integrated primary production ($P_{Z,t}$). In horizontally homogeneous systems, site-specific measures of $P_{Z,t}$ are simply extrapolated to the entire system to yield daily production. In large and heterogeneous aquatic systems, such as the ocean, phytoplankton production estimates are most often based on models which calculate depth- and time-integrated production from surface measures (i.e. Chl *a*) obtained through satellite imagery (i.e. Smith and Baker, 1978; Eppley et al. 1985). The majority of daily productivity models were developed for optically deep systems where the total depth of the water column equals or exceeds the euphotic depth, defined as the depth where irradiance reaches 1% of its surface value and as such, estimates of production are integrated over the entire euphotic zone (Behrenfeld and Falkowski, 1997). In shallow systems, where the theoretical euphotic depth, calculated from light attenuation coefficients, can exceed water column depth, existing models will therefore overestimate areal production.

Large rivers and estuaries frequently present complex bottom topographies where broad areas of littoral or subtidal shallows are separated by deeper channels, resulting in a spatially heterogeneous distribution of optical depths, or physical depths over which greater than 1% of irradiance is available. Although some models calculate production to a specified water depth (i.e. Platt and Sathyendranath, 1993) and some integration methods can correct for lake basin/river channel shape (i.e. Fee, 1990), these models require values of the photosynthetic parameters derived from P-I field measurements. Longitudinal gradients in physical, chemical and biological characteristics usually present in large fluvial or estuarine systems render an adequate spatial coverage based on field measures of productivity expensive and labour intensive. In such cases, a spatial approach based on remotely-sensed data measuring local physical and biological surface properties in combination with existing depth-integrated productivity models could provide more accurate estimate of whole-system production, compared with the approach of exptrapolating measured productivity from a few sites. The implementation of a spatial explicit approach would require, however, a correction model for varying optical depths.

Cole and Cloern (1987) found that in estuaries, daily euphotic zone production was linearly related to the composite variable $BZ_{eu}I_o$:

$$P_{Zeu,t} = c1\ BZ_{eu}I_o + c2 \quad (1)$$

where B is the mean phytoplankton biomass in the euphotic zone (mg Chl *a* m^{-3}), Z_{eu} is the euphotic depth (m) and I_o is the total daily surface irradiance (mol quanta m^{-2} d^{-1}), and c1 and c2 are empirical constants. The composite variable $BZ_{eu}I_o$ has been applied in numerous estuarine systems, where it explained between 32 % and 93 % of the variance in observed daily production (Cole and Cloern, 1987; Kromkamp et al. 1995; see Table 2 in Brush et al. 2002 for a summary of studies applying this model). Part of the unexplained variation in the relationship between observed euphotic zone production and $BZ_{eu}I_o$ could be due to the overestimation of areal production when theoretical euphotic depth exceeds water depth. Brawley et al. (2003) proposed a third-order polynomial model to correct Eq. 1 for cases where water depth (Z) is smaller than Z_{eu}. This correction is applicable only where water column depths are systematically shallower than Z_{eu}, however, and predicts unrealistic productions whenever Z exceeds Z_{eu}.

Here, a more general depth-correction is developed which is applicable to situations in which theoretical euphotic depth is either shallower or deeper than water depth. Although the correction can be applied to any daily productivity model estimating euphotic zone production, we present a modified composite model, which improved estimates of euphotic zone primary production compared to the original model of Cole and Cloern (1987). First, we describe the correction model and secondly, present an example of its use. We calculated spatially-explicit estimates of whole-system production corrected and uncorrected for depth to quantify the overestimation in production arising from shallow optical depths in a large fluvial lake of the St. Lawrence River (Quebec, Canada).

Methods

Study site: Lake St. Pierre (46° 12' N, 72° 49' W) is a large (~300 km^2), non-stratified broadening of the St. Lawrence River comprised of extensive shallow littoral zones (in which $Z_{eu} > Z$) as well as a deep, central channel (in which $Z_{eu} < Z$) (Figure 1 and 2). In

addition, light conditions vary markedly because of the presence of 4 main water masses with different clarity (light attenuation coefficients ranging from 0.5 to 5.3 m^{-1}) originating from various tributaries entering the river upstream of and within the fluvial lake (Figure 1). The physical complexity of Lake St. Pierre provides an opportunity to examine the effects of varying optical depths on areal and whole-system phytoplankton production estimates (Figure 2).

Depth-correction model: In a vertically homogeneous water column, areal daily production is a continuous non-linear function of integration depth (Figure 3) which can be modelled as a generalised von Bertalanffy growth equation of the form:

$$P_{Z,t} = P_{Zeu,t} (1 - e^{-KZ})^c \qquad (2)$$

where $P_{Z,t}$ (mgC m^{-2} d^{-1}) is daily production integrated between the surface and a specified depth (Z, m), $P_{Zeu,t}$ (mgC m^{-2} d^{-1}) is daily production integrated over the entire euphotic zone, K (m^{-1}) is the light attenuation coefficient, and c is an empirical constant. We used the product of K and Z, a dimensionless optical number rather than Z alone, to generalise the relationship to any water column. Median observed values in the St. Lawrence River (near Montreal - Blais, 2000; in Lake St. Pierre - Vis, 2004) for photosynthetic parameters P_{max} (maximum rate of light saturated photosynthesis) and α (initial slope of the P-I curve), light attenuation and surface irradiance were used to calculate daily areal production ($P_{Z,t}$) by numerical integration of production over depth and time. The resulting $P_{Z,t}$ vs. optical index data were fitted to Eq. 2 using non-linear regression (JMP 5.0, 1989-2002 SAS Institute Inc.) with the ratio of $P_{Z,t}$ to $P_{Zeu,t}$ as the independent variable since the asymptote ($P_{Zeu,t}$) is subject to the same error as $P_{Z,t}$.

Composite variable model: The composite model of Cole and Cloern (1987) (Eq.1) has been applied in many estuarine systems, however, its application within freshwater rivers has not yet been tested. Linear regression was used to derive the relationship between observed euphotic zone production and the composite variable $BZ_{eu}I_o$ (Eq.1) for data from the St. Lawrence River (Blais, 2000; Vis, 2004). The majority of stations sampled in this data set did not require depth correction (i.e. $Z > Z_{eu}$), so unexplained

variation was likely due to variables others than depth. This model lacks a photoadaptive variable and effects of temperature and nutrient conditions are not

Figure 1. Map of the Lake St. Pierre, St. Lawrence River (Quebec, Canada) showing the distribution of its major water masses. The boundaries of each water mass (solid white line) were outlined on a black and white Landsat TM image from September 21, 1984 and are from north to south: the north, mix, central and south water masses. The dotted line is the location of the cross-section presented in Figure 2.

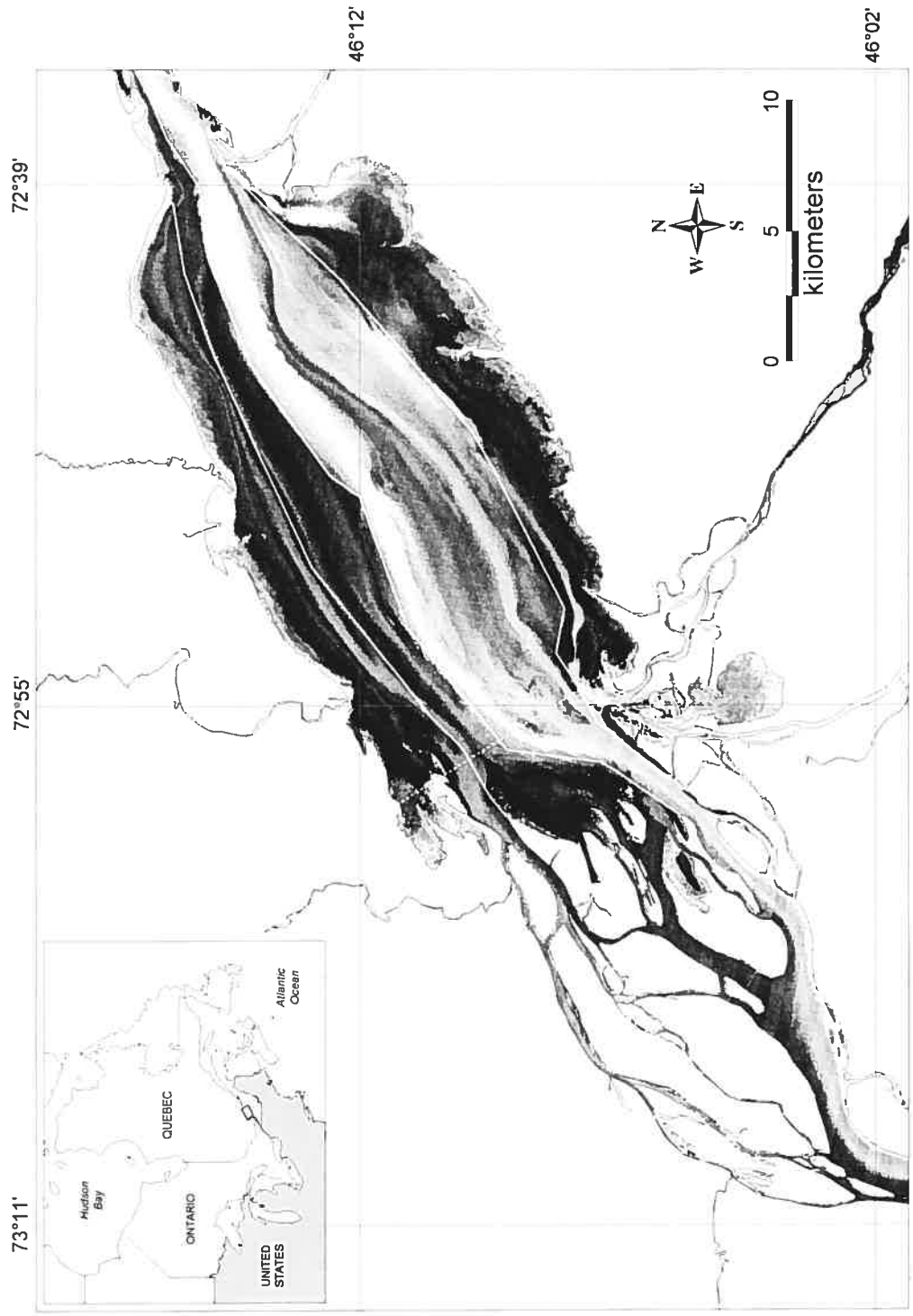

73°11'
72°55'
72°39'
46°12'
46°02'
N
E
S
W
0
5
10
kilometers
Hudson Bay
QUEBEC
ONTARIO
UNITED STATES
Atlantic Ocean

Figure 2. A bathymetric profile of a cross-section of Lake St. Pierre, St. Lawrence River. Boxes represent euphotic zone primary production in various regions of the lake; hatched area is the overestimation of areal phytoplankton production if estimates are uncorrected for optical depth. The distribution of the major water masses are indicated.

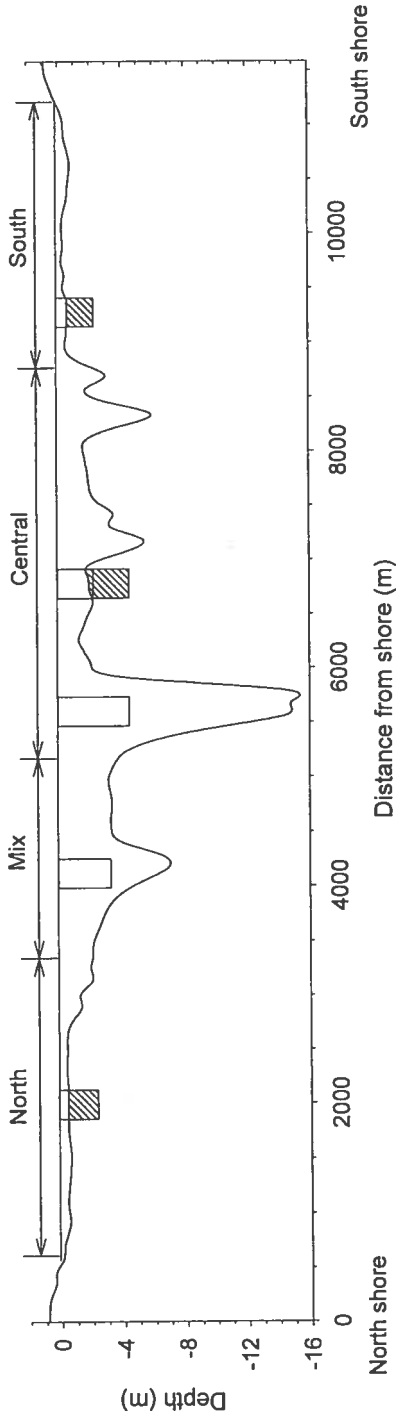

North
Mix
Central
South
0
-4
-8
-12
-16
Depth (m)
0
2000
4000
6000
8000
10000
Distance from shore (m)
North shore
South shore

Table 1. Data used in the example of the optical depth correction model applied to Lake St. Pierre, St. Lawrence River (June 2000). Mean biomass (B), light attenuation (K) and theoretical euphotic depth (Z_{eu}) calculated as 4.6 / K are presented for each water mass. Based on the mean depth of each water mass polygon, the ratio of theoretical euphotic depth to mean depth, euphotic zone production ($P_{Zeu,t}$) estimated from the composite variable $0.032xBZ_{eu}IoT$, areal production corrected for optical depth ($P_{Z,t}$) using Eq. 1, and the decrease in areal production resulting from the correction were calculated. A surface irradiance (I_o) of 40 mol quanta m^{-2} d^{-1} and a water temperature (T) of 16°C were used in all calculations.

Water mass	B (mgChla m^{-3})	K (m^{-1})	Z_{eu} (m)	mean Z (m)	Ratio (Z_{eu}:Z)	$PZ_{eu,t}$ (mg C m^{-2} d^{-1})	$P_{Z,t}$ (corrected) (mg C m^{-2} d^{-1})	% Correction
North	3.9	1.82	2.53	1.66	1.52	202	187	8
Mix	2.5	1.44	3.2	3.61	0.89	164	162	1.2
Central	2.5	1.02	4.51	4.45	1.01	231	227	1.8
South	11	2.01	2.29	0.98	2.34	516	410	25.8

considered in the model (Cole and Cloern, 1987). We added a fourth term, water temperature (T in °C) to the composite variable ($BZ_{eu}I_oT$) and derived the relationship between observed euphotic zone production and the modified composite variable using linear regression.

Application of the models: Estimates of phytoplankton production uncorrected and corrected for variable optical depths were compared for Lake St. Pierre using a GIS. We used the modified composite variable ($BZ_{eu}I_oT$) model to estimate euphotic zone primary production. Input variables were derived from field measures (B, K, I_o, T), remotely-sensed (B, K), topographic (Z) and calculated (Z_{eu} = 4.6/K) data. Several tributaries enter the St. Lawrence River upstream and within Lake St. Pierre, and there is relatively little lateral mixing of these different water masses. Each water mass has characteristic physical and chemical properties and can be distinguished visually from satellite images (Figure 1). Polygons of the 4 main water masses were outlined directly from a 21 September 1984 Landsat TM image, and were assigned a biomass (B, mg Chla m^{-3})and light attenuation coefficient (K) based on field measures from June of 2000 (Table 1). Although a Landsat image from June 2000 would have been more exact, discharge, the main factor controlling the spatial distribution of water masses was similar between 1984 and 2000 (11000 and 9600 m^3 s^{-1}, respectively). Polygons were converted to a grid with a pixel size of 25 x 25 m and all remaining analyses were done on raster-based maps. The bathymetric grid was obtained by adjusting a digital elevation map of Lake St. Pierre to mean water levels of June 2000. Spatially explicit calculations of euphotic zone primary production (i.e. 0.0032 x $BZ_{eu}I_oT$) and primary production corrected for variable optical depths using Eq.2 (with 0.0032x$BZ_{eu}I_oT$ as an estimate of $P_{Zeu,t}$) were made from grids of B and K, calculated Z_{eu} and bathymetry, and assuming a surface irradiance of 40 mol quanta m^{-2} d^{-1} and a water temperature of 16°C. Whole-system production was calculated by summation of individual pixels over the entire surface area.

Results

The relationship between areal daily production and the product of integration depth (Z) and light attenuation (K) presented a good fit to the generalized von

Bertalanffy growth equation (SE = 0.009, n = 47; Figure 3). Estimation of the constant (see Eq. 2) for the median values of P_{max}, α, K and I_o for the St. Lawrence River, yielded a value of 1.53 ± 0.02. Deviations of data from the fitted model were highest for small values of the optical number and near the euphotic depth, but were less than 3.5 % of euphotic zone primary production.

Although the original composite variable model explained a large part of the variation in euphotic zone primary production, the model was further improved by including water temperature. The original composite variable $BZ_{eu}I_o$ explained 77% of the variance in observed primary production in the St. Lawrence River (Figure 4A). This compares well with the performance of the composite variable model in estuaries where it explained 82 % of the variance in photic zone production (Cole and Cloern, 1987). The performance of the model increased by adding a fourth term, water temperature, to the composite variable (Figure 4B). The goodness of fit of the modified model was better than that of the original composite variable model ($r^2 = 0.85$ compared to 0.77) and the error decreased (SE = 60 mgC m^{-2} d^{-1} compared to 73).

Using the modified composite variable model as an estimate of euphotic zone primary production, we calculated areal phytoplankton production over the entire surface of Lake St. Pierre using Eq.2 and quantified the overestimation of phytoplankton production where water depth was less than theoretical euphotic zone depth (Table 1; Figure 5B and C).

The importance of correcting phytoplankton production estimates for varying optical depths varied spatially within the fluvial lake, with the overall effect of overestimating whole-system production by 22%. Depth corrections to areal phytoplankton production varied from <1 % in the deep channel areas to >150% in the very shallow (depth < 50cm) littoral regions of Lake St. Pierre (Figure 5C). Based on mean water depths within each water mass, depth corrections were most important in the south (25 % correction) and north (8 % correction) water masses, due to the wide expanses of gently sloping shores present in these areas (Table 1). Spatial variations in depth-correction were also important within a single water mass. For example, within the central water mass, shoals present adjacent to the main channel in the upstream region of the lake presented high values of corrections (25-50%; Figure 5C), whereas no

Figure 3. Relationship of integrated daily production ($P_{Z,t}$) and optical number (K x Z; light attenuation times integration depth). $P_{Z,t}$ was calculated at increasing depths by increments of 0.1 m between the surface and 4 m and by increments of 1 m between 4 m and 10 m, for the median observations in photosynthetic parameters and light in the St. Lawrence River (open circles). Representative values of the median conditions in the St. Lawrence River used were; P_{max} = 11 mg C m^{-3} h^{-1}, α = 12 mg C mol quanta^{-1} m^{-2}), light attenuation K= 1.3 m^{-1} and daily surface irradiance I_o = 40 mol quanta m^{-2} d^{-1}). The data were fit to a generalized von Bertalanffy growth equation (solid line: see text for details).

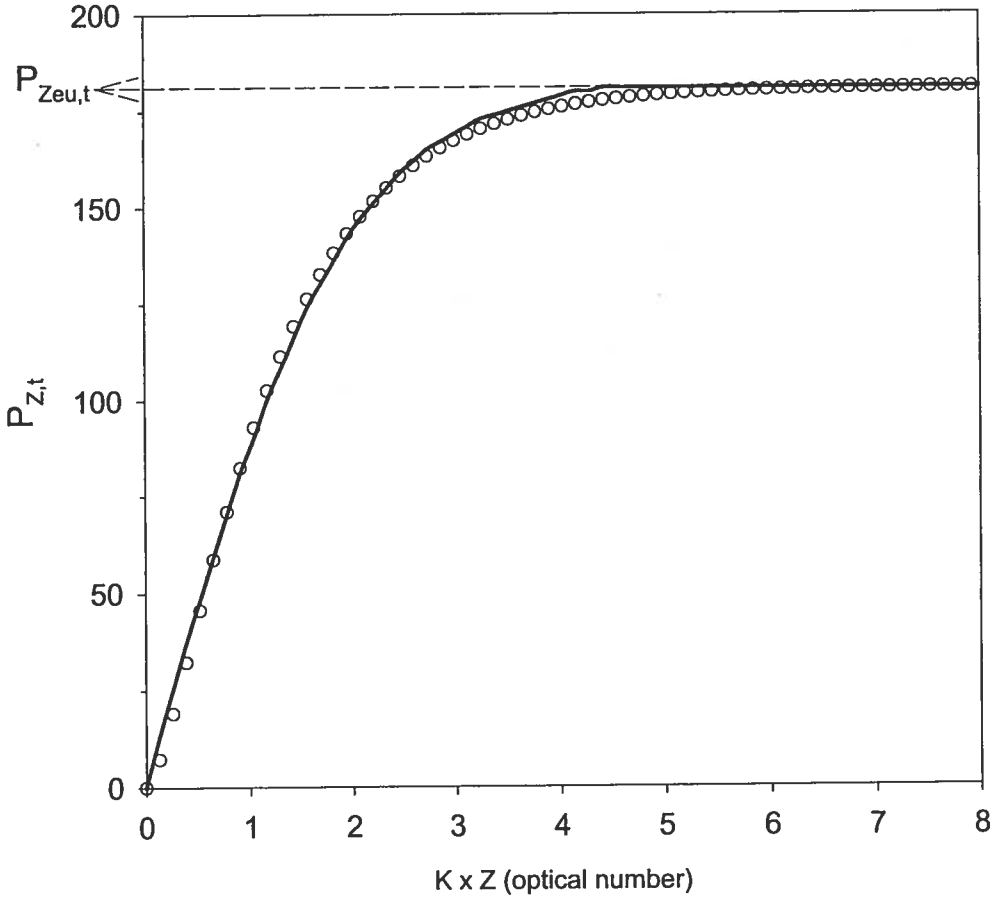

200
150
100
50
0
$P_{Zeu,t}$
$P_{Z,t}$
0
1
2
3
4
5
6
7
8
K x Z (optical number)

Figure 4. Observed and predicted euphotic zone primary production (mgC m^{-2} d^{-1}) for the St. Lawrence River. Predicted production was calculated from A) the original composite variable linear regression model (Eq.1) applied to the St. Lawrence River data and from B) the modified composite variable linear regression model which includes a fourth term, water temperature (T). The intercepts of both linear regression models were not significantly different from zero ($p < 0.05$, Student's T-test using asymptotic standard errors) and, thereby not used in the models.

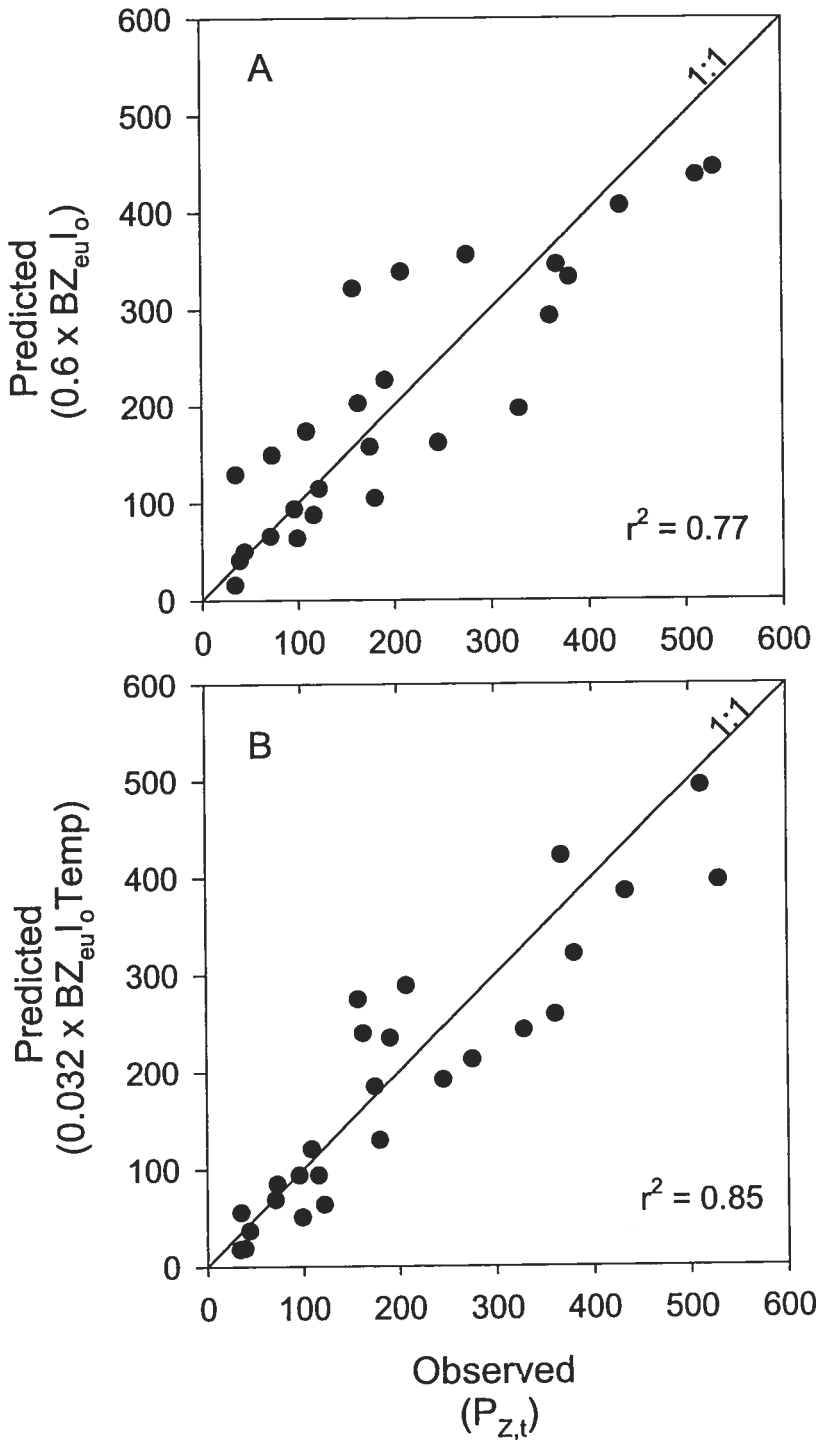
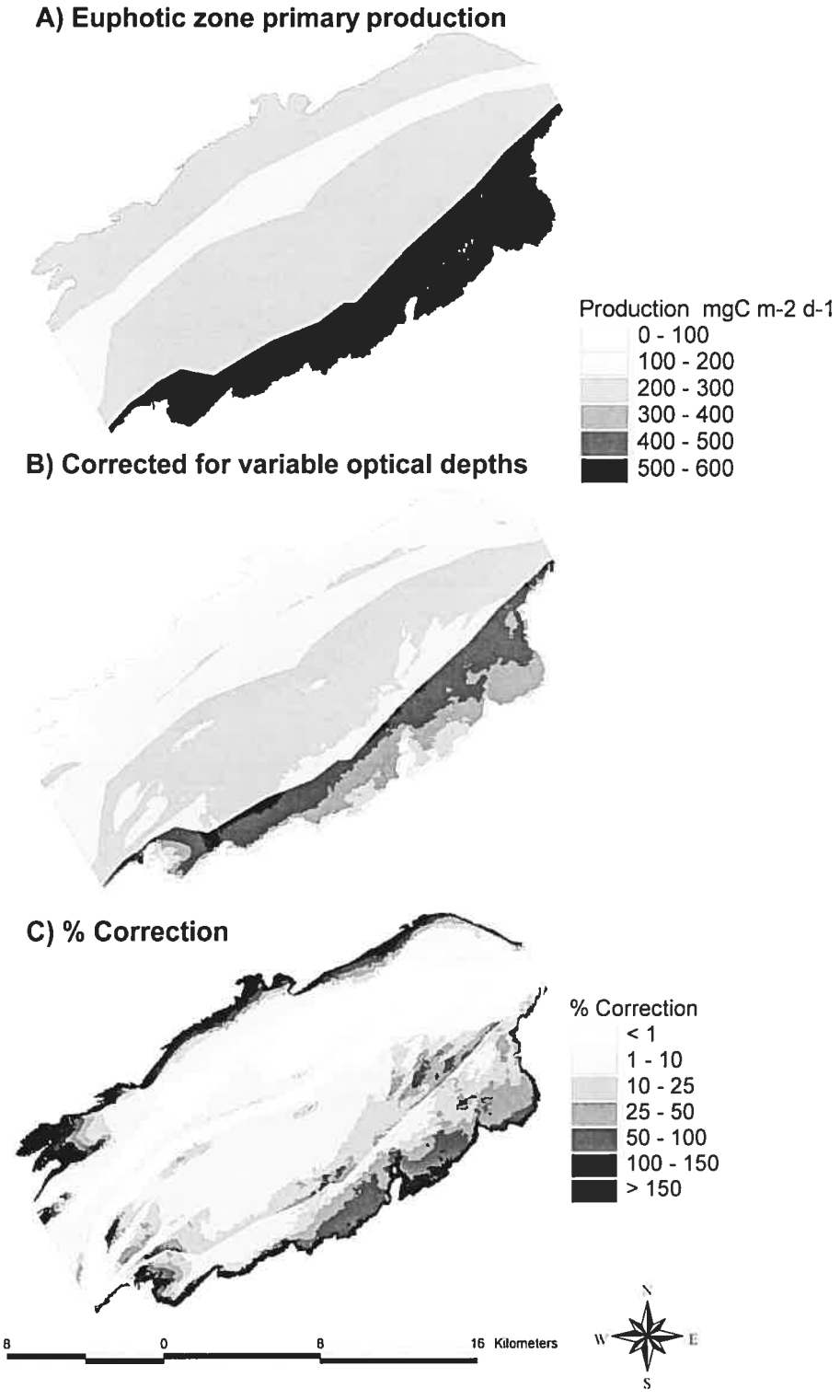

A
1:1
r^2 = 0.77
Predicted
(0.6 x $BZ_{eu}I_o$)
B
1:1
r^2 = 0.85
Predicted
(0.032 x $BZ_{eu}I_oTemp$)
Observed
($P_{Z,t}$)
0
100
200
300
400
500
600

Figure 5. Estimates of areal phytoplankton primary production uncorrected (euphotic zone primary production) (A) and corrected for variable optical depth (B) and the percent correction (% decrease) to areal phytoplankton production (C) for Lake St. Pierre, St. Lawrence River (June 2000).


A) Euphotic zone primary production
Production mgC m-2 d-1
0 - 100
100 - 200
200 - 300
300 - 400
400 - 500
500 - 600
B) Corrected for variable optical depths
C) % Correction
% Correction
< 1
1 - 10
10 - 25
25 - 50
50 - 100
100 - 150
> 150
8
0
8
16 Kilometers
N
W
E
S

correction was necessary within the main channel. Whole-lake phytoplankton production uncorrected was 82.8 m.t. C d^{-1}, compared to 68.0 m.t. C d^{-1} corrected for variable optical depths, resulting in an overestimation of whole-lake production of 22 %.

Discussion

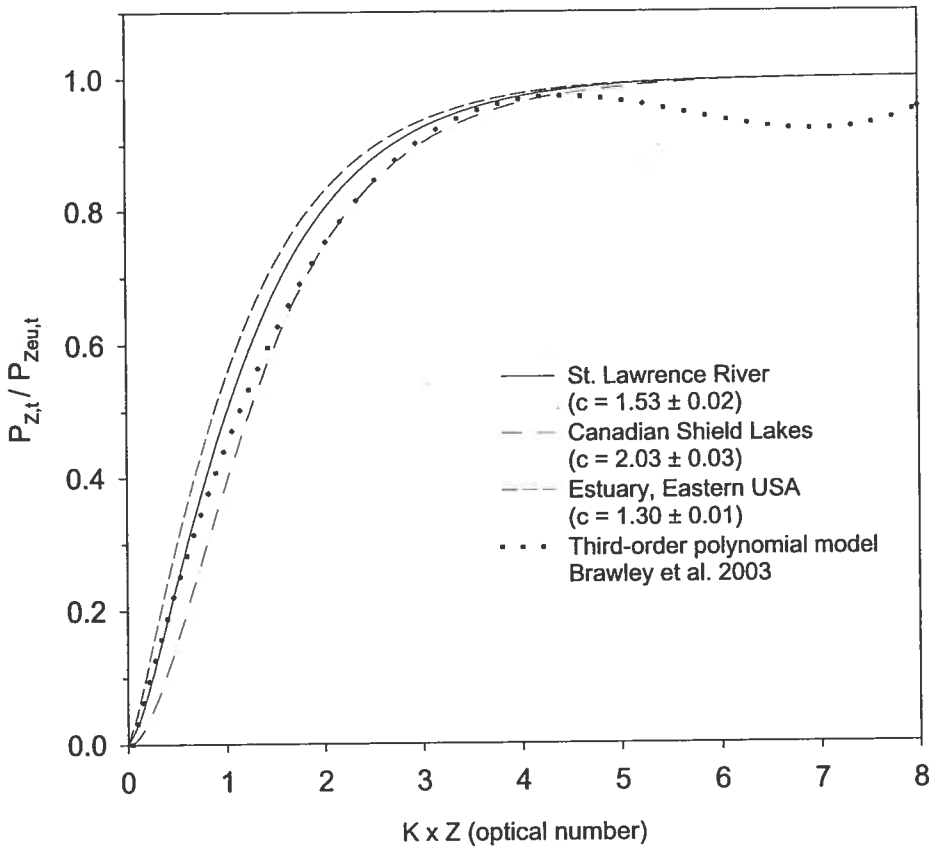
This study shows the importance of accounting for variable optical depths when estimating areal phytoplankton production in large, shallow water ecosystems. Whole-lake areal production uncorrected for morphometry was 22 % higher than production corrected for optical depth in Lake St. Pierre. Areal estimates without correction in the shallow regions of the lake ($Z < 1$ m) overestimated primary production by > 95%, and this shallow area accounts for 20 % of the total surface area of Lake St. Pierre. If this shallow zone was excluded, depth-corrections to areal production averaged 7% but ranged from 0 to 95%. In Lake Ontario and Lake Erie, depth corrections were on average low (2.3 - 6.4 %) but at some stations reached as high as 40 % (Millard et al. 2000). In small lakes, areal primary production can by overestimated by up to 20% if uncorrected for depth (Fee, 1980). The relative importance of depth corrections varies with the size and depth of the system and with transparency, however, reliable estimates of areal phytoplankton production and spatially explicit estimates of production in large shallow systems, such as estuaries and large rivers require correction for variable optical depths.

The correction model developed here is calculated from water depth and light attenuation, however, the relationship between $P_{Z,t}$ and optical number (K x Z) is also influenced by the photosynthetic parameters (P_{max}, α) and surface irradiance, and estimates of the empirical constant of the depth correction model will vary with the fitted data. To examine the possible range in values of the fitted constant, we calculated estimates of c for median observed conditions in P_{max}, α, K and I_o in an Eastern United States Estuary (Cheasepeake and Delaware Bays-Harding et al. 1986) and for a series of lakes in Quebec (Carignan et al. 2000) (Figure 6). The range in photosynthetic parameters based on the median observations was 8 - 35 mg C m^{-3} h^{-1} for P_{max} and 12 - 46 mg C mol quanta^{-1} m^{-2} for α, and between 0.65 and 1.3 m^{-1} for K and 20 - 40 mol quanta m^{-2} d^{-1} for I_o. Estimates of c were significantly different ($p < 0.05$, Student's T-

tests using asymptotic standard errors), however, differences between the various curves generated relatively minor differences in the amount of depth correction (averaged 3 % of euphotic zone primary production). Error on depth correction will, however, be higher for light and photosynthetic conditions which differ from the median observations. Clearly, the most accurate depth correction model would be obtained by estimating the constant for specific conditions in photosynthetic parameters and light prevailing over given seasons or within aquatic systems. This information, however, is often not available and costly to obtain, and when available, a direct integration of production would yield the most precise estimate of production. The range in light conditions and photosynthetic parameters used in Figure 6 could be used as a guide to determine which constant to use in the depth correction model for the various types of systems in temperate regions. Considering depth corrections can be as high as 40% (Millard et al. 2000) or > 95% in Lake St. Pierre, the error generated by depth-correction model due to the value of the constant are small in comparison.

The composite variable $BZ_{eu}I_o$ explained a large part of the variability in observed production in the St. Lawrence River. Similar to estuarine systems, large rivers are often nutrient-rich and well-mixed, and phytoplankton primary production in this type of system seems to be largely influenced by biomass and irradiance. Physiological variability in the photosynthetic response of phytoplankton to nutrient availability and temperature were secondary controls on phytoplankton production in estuaries and thereby no photoadaptive variable was included in the original model of Cole and Cloern (1987). In the St. Lawrence River, seasonal changes in photosynthetic response and consequently production were much larger than seasonal variations in biomass and were partly related to water temperature (Blais 2000). Water temperature influences photosynthetic parameters and growth (i.e. Eppley 1972) and is easily measured in the field or by remote sensing compared with the more costly and time consuming measures of productivity. By adding this variable to the composite variable of Cole and Cloern (1987), the model was improved explaining 85% of the variation in production in the St. Lawrence River, at the same time remaining simple and calculable from available biomass, light and temperature data.

Figure 6. Comparison of the depth correction model fit to data from the St. Lawrence River with the model fit to data from two other aquatic systems, a series of Canadian Shield Lakes (dash-dotted line) and Chesapeake and Delaware Bays (dashed line). Median values of photosynthetic parameters and light conditions for Canadian Shield Lakes and Chesapeake and Delaware Bays were calculated from data presented in Carignan et al. 2000 and Harding et al. 1986, respectively. The estimates of the fitted constant are presented on the figure. The depth correction model based on a third-order polynomial of Brawley et al. 2003 is also shown (dotted line).


1.0
0.8
0.6
0.4
0.2
0.0
$P_{Z,t} / P_{Zeu,t}$
0
1
2
3
4
5
6
7
8
K x Z (optical number)
St. Lawrence River
(c = 1.53 ± 0.02)
Canadian Shield Lakes
(c = 2.03 ± 0.03)
Estuary, Eastern USA
(c = 1.30 ± 0.01)
Third-order polynomial model
Brawley et al. 2003

Although we used the composite variable model, the depth-correction model can be applied to any productivity model estimating euphotic zone primary production. Depth-integrated productivity models vary from simple formulations which calculate $P_{Zeu,t}$ as a function of surface chlorophyll to more elaborate calculations requiring estimates of euphotic depth, daily integrated PAR, irradiance-dependent functions and photoadaptive parameters (see review by Behrenfeld and Falkowski, 1997). In addition, production estimates can be adjusted for variable mixed layer thickness using the depth correction model. Vertical mixing depths can be shallower than theoretical euphotic zone depth at various time of the year in aquatic systems. In these cases, integrated productivity is often calculated over the mixed layer only (i.e. epilimnetic production in lakes), and by substituting mixed layer depth for water depth (Z) in the depth correction model, production estimates are corrected for the overestimation.

In short, the depth-correction presented is a general model which can adjust estimates of the euphotic zone primary production ($P_{Zeu,t}$) for water depth or mixing depth shallower than the theoretical euphotic depth, thereby adapting existing daily productivity models for application within shallow water systems. The use of this model will allow for increased spatial and temporal modelling of algal production in diverse shallow water systems.

Acknowledgements

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CHAPITRE 3

Variations in photosynthesis and respiration by periphyton and filamentous algal mats in a fluvial lake of the St. Lawrence River: implications on estimates of areal production

Vis, C., C. Hudon, & R. Carignan. Variations in photosynthesis and respiration by periphyton and filamentous algal mats in a fluvial lake of the St. Lawrence River: implications on estimates of areal production. *Canadian Journal of Fisheries and Aquatic Sciences*. Submitted.

Abstract

The photosynthesis-irradiance (P-I) relationship was examined for periphyton growing on artificial substrata placed within macrophyte stands and masses of filamentous algae (FAM) in Lake St. Pierre, a large (about 300 km^2) broadening of the St. Lawrence River. Study sites were chosen to present a range of depth, temperature, light and chemical conditions to determine the effects of environmental variables on whole-assemblage photosynthetic parameters and dark respiration. Photosynthetic parameters including the maximum rate of biomass-specific photosynthesis (P_{max}^B), the initial slope of the photosynthesis-irradiance curve (α^B) and saturation PAR (I_k) were on average higher for FAM than for periphyton, indicating filamentous algal mats utilised light more efficiently than attached algae. For periphyton, photosynthetic parameters were positively correlated with each other, whether expressed per unit biomass or per unit area of substratum ($r = 0.51 - 0.74$, $p < 0.0001$). Biomass had the strongest influence on photosynthetic parameters ($r^2 = 0.33 - 0.72$), although additional variation in the maximum rates of photosynthesis was explained by *in situ* light levels and temperature ($r^2 = 0.56 - 0.84$). Dark respiration rates were best related to photosynthetic parameters ($r^2 = 0.30 - 0.76$), suggesting a coupling between autotrophic and heterotrophic processes within the biofilm. Sun-shade photoadaptation responses were sometimes observed between samples from shallow and deep water and P_{max}^B was positively correlated to *in situ* light. Simulations of integrated areal production demonstrated that neglecting depth variations in the distribution of periphyton biomass and photosynthetic response within a macrophyte stand can result in errors on estimates of areal production of up to 50 %. Results emphasise the importance of integrating the vertical complexities in light and biomass of macrophyte stands when scaling-up estimates of periphyton production, to determine its contribution to whole-system production.

Introduction

Despite the common occurrence of vascular plants in lakes and flowing waters, productivity estimates of algae attached to macrophytes (epiphyton) remain relatively sparse, particularly at the ecosystem level. Compared to phytoplankton, the study of photosynthesis by attached microbial communities presents additional difficulties linked

to the extreme vertical and horizontal heterogeneity in biomass, substrate availability, light level and turbulence across spatial scales ranging from micrometres to kilometres. Because periphyton may account for an important portion of primary production and energy flow to higher trophic levels in aquatic systems (i.e. Hecky and Hesslein 1995; Vadeboncoeur et al. 2001), estimates of periphyton production which integrate vertical and horizontal heterogeneity are required to obtain realistic estimates of the contribution of periphyton to whole-system production.

The estimation of areal production by periphyton can be approached in a manner analogous to that used for phytoplankton, where photosynthesis versus irradiance (P-I) curves, vertical biomass and irradiance profiles are combined to produce numerically integrated estimates of daily production per m^2 of lake area (Jones 1984). Although photosynthetic parameters (the maximum rate of photosynthesis at light saturation, P_{max} and the initial slope of the P-I curve, α) derived from natural periphyton assemblages have little physiological meaning due to substrate complexity and self-shading effects within the biofilm, these properties can be used to compute time- and depth-integrated areal production. Photosynthetic parameters for attached algae and their dependence on environmental conditions are still poorly known, however (Vadeboncoeur and Steinman 2002).

Variable photosynthetic responses with depth or shade adaptation has been observed within the periphyton matrix using micro-electrode techniques (e.g. Sand-Jensen and Revsbech 1987, Dodds et al. 1999) and for whole-assemblages (e.g. Cattaneo and Kalff 1980, Kairesalo 1983, Müller 1995). Biomass has been shown to have a strong influence on whole-assemblage photosynthetic rates in benthic algae (e.g. Marker 1976; Hill and Boston 1991; Müller 1995), and to vary with depth in epiphyton communities on emergent (Kairesalo 1983; Meulemans 1988; Burkholder and Wetzel 1989, Müller 1995), floating-leaved (Romo and Galanti 1998) and submerged macrophytes (O'Neill Morin and Kimball 1983). One study found that variations in the vertical distribution of epiphyte biomass on submerged species of macrophytes could result in over or under estimations of areal production of up to 53%, depending on macrophyte growth forms and light availability (Hart and Lovvorn 2000). The cumulative impact of depth variations in biomass, in .light conditions and in the

photosynthetic response of epiphyton within macrophyte stands on the estimate of production expressed on a per unit area of bottom surface basis and the resulting error propagated onto whole-system estimates of production remain poorly quantified.

Filamentous algal mats (FAM), initially grow attached to macrophytes and other surfaces and, if masses are large, eventually, detach to form floating mats. Such mats provide alternative habitats for invertebrates (Power 1990; Norkko et al 2000) and strongly influence primary production (e.g. Robinson et al. 1997). So far, most studies have focused on *Cladophora* (Dodds and Gudder 1992), even if algal mats can be dominated by other species (e.g. *Enteromorpha*, *Mougeotia*, *Oedogonium*, *Spirogyra* and *Stigeoclonium*; Goldsborough and Robinson 1996; Nozaki 2001). The photosynthetic response of these communities (P-I curve) have not yet been studied in direct comparison with attached forms of algal.

In this study, we compare the photosynthetic parameters and dark respiration of periphyton among sites with markedly different physical (e.g. light, depth) and chemical characteristics (e.g. nutrients, DOC) to determine the effects of environmental variables on whole-assemblage metabolism. We compare the photosynthetic response of attached vs filamentous algae. Finally, we examine how depth variations in photosynthetic response and biomass of periphtyon within different types of macrophyte stands will in turn, influence estimates of daily integrated (time and depth) production estimates per unit area of bottom surface. The simulation modeling will then be discussed in the context of spatial extrapolation of field data to the determination of whole-system production.

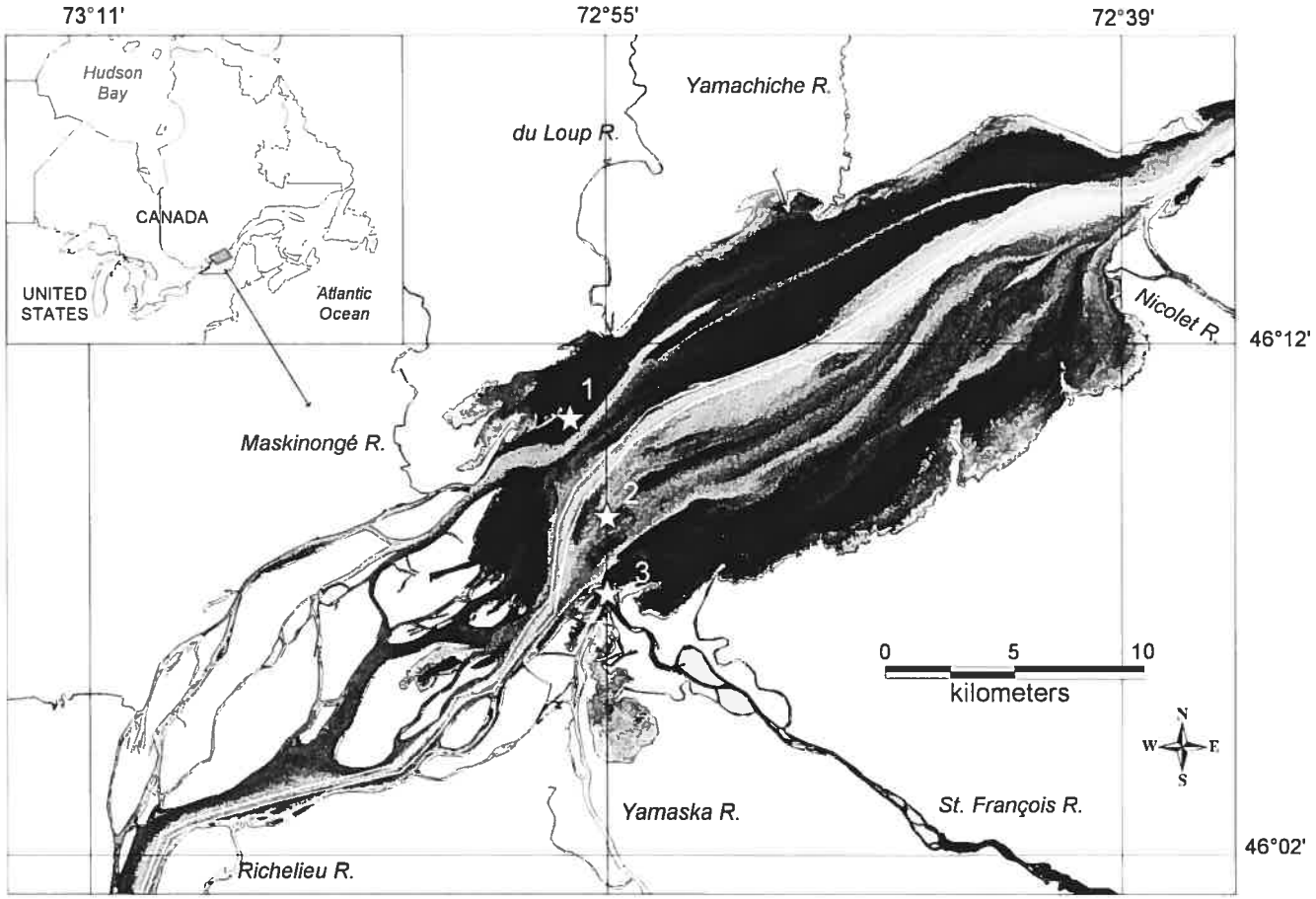
Methods

Study site- Lake St. Pierre is a large (~300 km^2) broadening of the St. Lawrence River (mean annual discharge: 11 500 m^3 s^{-1}) located 100 km downstream of Montreal, Canada (46° 12' N, 72° 49' W). The lake is shallow over most of its surface area (mean depth < 4 m) with the exception of a deep navigation channel located in the middle of the lake (Figure 1). Several tributaries impacted to varying degrees by agriculture join the river upstream or within Lake St. Pierre. The plume of these rivers flow side by side with little lateral mixing, thereby creating a spatially complex system (Figure 1). The

gently sloping shores of Lake St. Pierre have favoured the development of large expanses of emergent and submerged rooted aquatic vegetation (macrophytes) which cover approximately 3/4 of the lake's surface area.

We studied periphyton productivity at three sites located within three major water masses between June and October of 2000 and 2001 in order to cover a wide range in physical and chemical properties (e.g. depth, light, nutrients) expected to influence periphyton metabolism (Figure 1, Table 1). Site 1 was located in DOC-rich, brown waters originating from north shore tributaries, principally the Ottawa River and was colonized by a moderate biomass of macrophytes comprising an understory of *Vallisneria americana* Michx. with a sparse canopy of *Potamogeton richardsonii* (A. Bennett) Rydb. Site 2, located in relatively clear waters originating from the Great Lakes, was colonised by *Stuckenia pectinata* L. (formerly *Potamogeton pectinatus* L.) in early spring, which was later succeeded by *Vallisneria americana* and *Potamogeton richardsonii*. Site 3 (2001 only) was under the influence of brown and heavily enriched waters originating from the Yamaska River. This site, located in relatively shallow water (< 0.6 m), was colonized by dense submerged vegetation reaching the surface (*Vallisneria americana* and *Potamogeton richardsonii*) interspersed with sedges and cattails (e.g. *Schoenoplectus lacustris* (L.) Pallu, *Typha angustifolia* L.). At all sites, macrophytes appeared in June, reached their maximum biomass in mid-August, and died back in mid-September of each year, with the exception of *Stuckenia pectinata* which reached its maximum biomass in July and senesced in August.

Figure 1. Map of study sites located in Lake St. Pierre, St. Lawrence River overlying a black and white Landsat TM image (21 September 1984) which shows the distribution of the major water masses. Site 1 (north water mass) and 2 (central water mass) were sampled in 2000 and 2001, site 3 (south water mass) was added in 2001. The deep central navigation channel is outlined.


73°11'
72°55'
72°39'
Hudson Bay
CANADA
UNITED STATES
Atlantic Ocean
Yamachiche R.
du Loup R.
Nicolet R.
46°12'
1
2
3
Maskinongé R.
0
5
10
kilometers
N
W
E
S
Yamaska R.
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46°02'

Environmental variables – In situ environmental conditions were measured at the time of sampling at each site to characterise the different sites and assess the influence of some of these variables on respiration and photosynthetic parameters. Water temperature, conductivity and pH (Hydrolab MiniSonde 4a; Austin, Texas, USA) and current velocity (Marsh-McBirney FloMate model 2000; Frederick, Maryland, USA) were measured 20 cm below the surface on each sampling date. We also collected 2 L of water, one part of which was filtered (300 - 1000 mL) onto Whatman GF/C filters (pore size 1.2 μm) and frozen to determine planktonic chlorophyll a, and the other part used to measure suspended solids and colour. Chlorophyll a was determined spectrophotometrically following filtration (Whatman GF/C) and 24 h extraction at 4°C of the frozen filters in 95% ethanol and calculated using the equations of Nusch (1980). Suspended solids were determined by filtration (100-800 ml) through pre-combusted, pre-weighed Whatman GF/C filters (APHA 1998). Colour was determined spectrophotometricallly as absorption at 440 nm of filtered water (Whatman GF/C) (Cuthbert and Del Giorgio 1992). The *in situ* light intensity (PAR) was measured within macrophyte stands using a surface LiCor LI-190SA and submersible LI-193SA spherical sensor. Light measurements were made without disturbing the canopy by attaching the underwater light and a pressure sensor to the end of a pole which was lowered obliquely into the macrophyte stand. An average PAR attenuation coefficient (K) for the water column (including the shading effect of dense macrophytes) was calculated from 3-6 profiles at each site. The light conditions of samples was also characterized using the incident irradiance (I_0) on sampling days as well as the mean incident irradiance over the 3 (I_3) and 5 (I_5) days prior to sampling. Incident PAR was recorded continuously (LI-190SA) at a field station located 100 km north of Montreal in 2000 and at a field station adjacent to Lake St. Pierre in 2001 between June and September of each year. Daily water levels were obtained for the nearest gauging station (Lake Saint-Pierre Curve no. 2, no. 15975, Marine Environment Data Services, Department of Fisheries and Oceans of Canada); level data was referenced to the International Great Lakes Datum of 1985 (m above sea level, IGLD85).

Production and respiration - Measurements were made on periphyton colonizing artificial substrata installed at each site at the beginning of the growth season in early June. Artificial substrata were used to allow for the use of the oxygen method to measure whole-assemblage gross production and respiration rates. Artificial substrata were made of ~3 x 10 cm clear polyethylene rectangles tied at 20 cm intervals to 1 to 3 m-long strings of nylon monofilament. The strings were anchored to the bottom and a cork tied to the upper end maintained the artificial substrata in a natural attitude in the water column. At site 3, plastic rods (diameter 0.85 cm) mimicking the stems of emergent vegetation were pushed into the sediments. Low water levels in July-August 2001 prompted the addition of substrata at sites 2 and 3, resulting in the addition of a variable describing the time of submergence (periphyton development time) in the analysis.

Photosynthesis (P) and respiration (R) were measured at approximately monthly intervals between late June and September of each year using an adapted oxygen method. Artificial substrata (6 to 9 strings) were collected by divers, kept at *in situ* temperatures and processed within 6 h at a nearby field laboratory. The height of the artificial substrata in the water column was noted in the field to determine the sampling depth of individual rectangles used for P and R measurements. Water used for incubations was collected on site, filtered (Whatman GF/C) and distributed into clear 300-ml pyrex bottles. We ensured that all bottles used in a given experiment had identical (± 0.01 mg L^{-1}) initial oxygen concentrations by distributing the filtered water from a 20 L polyethylene tank in which a floating cover prevented gas exchange during the filling operation; water was delivered at the bottom of each bottle, allowing for a two-volume overflow. One plastic rectangle was inserted into each bottle (after removal of macroinvertebrates) and the bottles were placed in a temperature-regulated, rotating wheel incubator (Shearer et al. 1985) equipped with a Phillips MH1000 1000-watt metal halide lamp. Duplicate or triplicate samples were incubated at *in situ* temperatures (± 1°C) during two to five hours under five light intensities ranging between 20 and 1000 µmol quanta m^{-2} s^{-1}. Periphyton community respiration was measured from incubation of artificial substrata in dark bottles. PAR irradiances were measured (Biospherical QSL-100 quantum meter) at each level of light intensity (incubator wheel) during every

incubation. Triplicate BOD bottles incubated without artificial substrata served to measure initial dissolved oxygen concentration. At the end of the incubation, dissolved oxygen was measured in each bottle using a YSI model 5905 self-stirring oxygen probe calibrated in water-saturated air at local barometric pressure. Plastic rods colonized by periphyton within stands of emergent macrophytes were cut into 5-cm segments and treated as above. Photosynthesis and respiration by FAM were measured on eight occasions using the same procedure. Small samples of FAM were preserved in Lugol for identification of dominant genus.

Net primary production (NPP) and community respiration (R_{com}) were calculated from the changes in oxygen concentration during the incubations. Gross primary production (GPP) was calculated as NPP + R_{com}. Production and respiration rates were expressed either per unit of area, of biomass (mg Chl *a*), or per unit of artificial substratum available for colonization (periphyton only). Periphyton biomass on artificial substrata was determined by extracting pigments directly from rectangles of plastic or rods, frozen whole after incubation. Clumps of FAM were also placed directly into extraction tubes and frozen until analysis. Epiphytic Chl *a* detached from the substrates during incubation was recovered by filtering (Whatman GF/C) the content of incubation bottles. Chlorophyll *a* was determined spectrophotometrically following 24 h extraction at 4 °C of the frozen filters in 95% ethanol and calculated using equations of Nusch (1980). The surface area of individual rectangles and rods of artificial substrata were calculated from measurements of length and width or diameter and in the case of plastic rectangles, assuming both sides of the substratum were available for colonization.

Data analysis - P_{max}, the maximum rate of light-saturated gross photosynthesis, and α, the initial slope, were estimated from the fit of *P-I* data to the hyperbolic function of Jassby and Platt (1976). Both photosynthetic parameters were expressed per unit biomass (P_{max}^B, α^B) and per unit area (P_{max}^A, α^A). The saturation parameter I_k, was calculated as P_{max} / α. A photosynthetic quotient of 1.2 was used to convert P and R data from oxygen units into carbon equivalents (Wetzel and Likens 2000).

Data were normalized using a $\log_{10}$-transformation prior to statistical analyses. Differences in environmental variables between sites, in photosynthetic parameters

between types of algal community (periphyton vs. FAM) and with depth were assessed using one-way analyses of variance. Differences among sites were examined using Tukey-Kramer tests on means. Relationships between photosynthetic parameters, biomass, respiration and environmental variables were quantified using parametric correlations (Pearson r), simple and multiple regressions.

Modelling of time and depth integrated epiphyton production - To examine the effects of depth variations in the distribution of epiphyton biomass and photosynthetic response on estimates of areal epiphyton production (per m^2 of bottom area), we calculated time and depth-integrated epiphyton production (mgC m^{-2} d^{-1}) for macrophyte stands of various types and growth forms. Four hypothetical macrophyte stands with a variable allocation of biomass, and consequently different surface area available for colonization by epiphytes were considered. The vertical distribution of epiphyte biomass for each stand type was estimated on the basis of previously reported macrophyte depth distributions of submerged species (Titus and Adams 1979; C. Hudon, unpublished data) or was approximated for emergent and floating-leaved species, to correspond to an equivalent areal epiphyton biomass of 100 mgChl *a* m^{-2} of bottom area. For each of the four scenarios, areal epiphytic production was calculated assuming a constant photosynthetic response with depth (P_{max}^B = 1.2 mgC (mgChl a^{-1}) h^{-1}, α^B = 0.007 mgC (mgChl a^{-1}) h^{-1}(μmol^{-1} m^{-2} s^{-1}) $^{-1}$)), and a variable photosynthetic response in the top versus bottom portion of the stand (P_{max}^B - 1.6 : 0.8 mgC (mgChl a^{-1}) h^{-1}, α^B - 0.003:0.0011 mgC (mgChl a^{-1}) h^{-1}(μmol^{-1} m^{-2} s^{-1}) $^{-1}$ for different light attenuations (K = 1 - 5 m^{-1}) in the water column. Time and depth-integrated epiphyton production (mgC m^{-2} d^{-1}) were calculated according to Jones (1984) or using the same numerical integration methods as applied to phytoplankton (Fee 1990). Specifically, daily production was calculated by integrating the following relationships over time (by 30 min. intervals) and depth (by 20 cm depth strata): 1) depth distribution of algal biomass, 2) P-I relationships 3) light attenuation with depth and 4) diurnal variations in surface irradiance assuming a daily irradiance of 35 mol quanta m^{-2} d^{-1} (average daily PAR during our study) for a 0.8 m-deep water column.

Results

Environmental characteristics of sites - The three study sites differed with respect to their chemical and physical characteristics (Table 1). Sites 1 and 3 were characterised by coloured, DOC- and nutrient-rich waters, in contrast with site 2 which had relatively clear (low colour and suspended solids), more mineralised waters with low DOC concentrations. Nutrients, DOC, suspended solids and planktonic chlorophyll a concentrations were highest at site 3. Average current velocity, light and temperature did not differ between sites 1 and 2, but very high light attenuation coefficients (K = 9 - 13 m^{-1}) were observed at site 3 due to the combination of water characteristics (high suspended solids and colour values) and dense macrophyte cover.

Table 1. Range in environmental variables (mean ± s.d.) observed at the study sites in Lake St. Pierre between June and September of 2000 and 2001. Significant differences between sites are indicated by different lowercase letters; *a*, *b* and *c*, (Tukey-Kramer test).

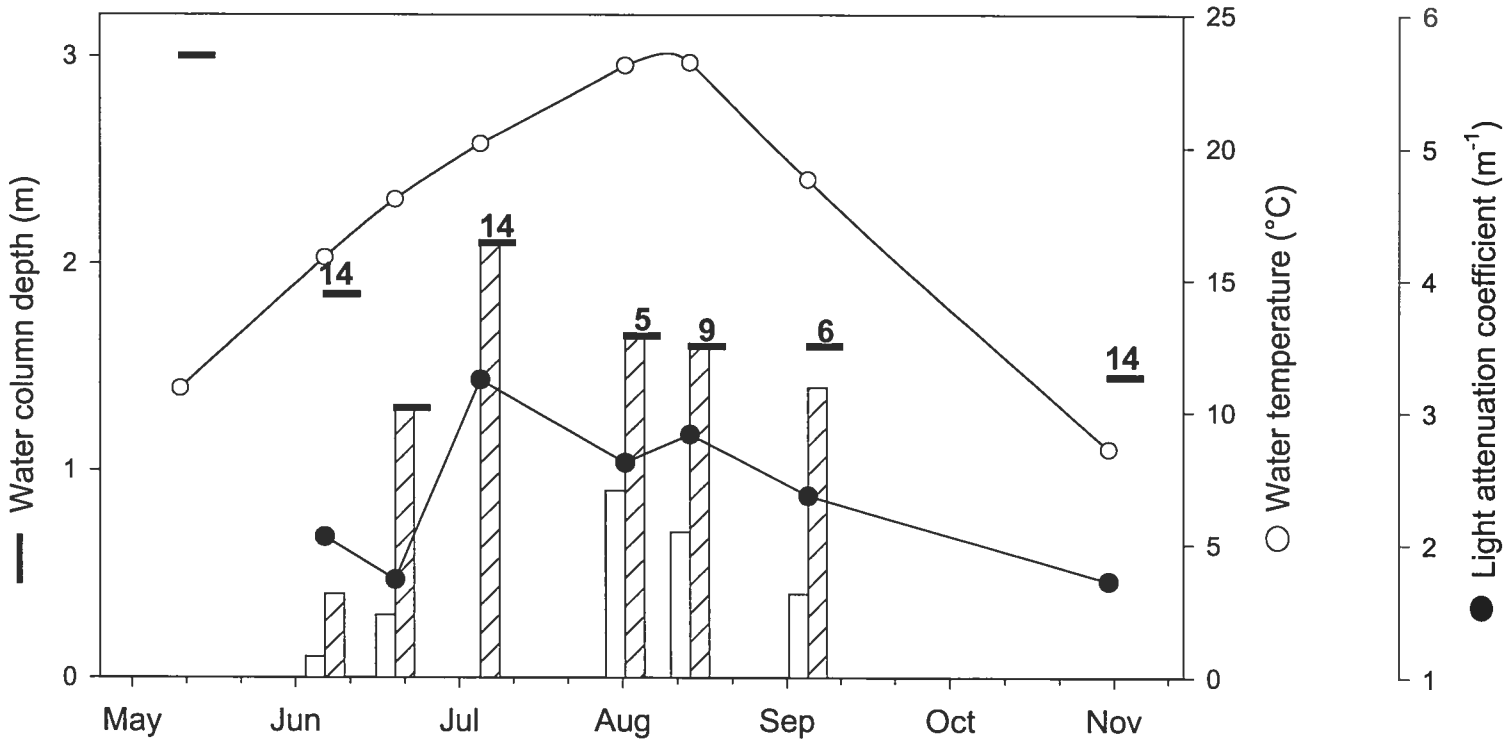
Variable	Site 1 (n = 8)	Site 2 (n = 8)	Site 3 (n = 4)
Depth (m)	1.4 ± 0.4^a	1.6 ± 0.5^a	0.5 ± 0.1^b
Current velocity(m s^{-1})	0.05 ± 0.05	0.09 ± 0.09	0.04 ± 0.05
Light attenuation coefficient (m^{-1})	2.98 ± 0.83^b	2.37 ± 0.84^b	10.93 ± 1.46^a
Temperature (°C)	21 ± 2	21 ± 2	22 ± 3
Specific conductivity (µS cm^{-1})	168 ± 37^b	229 ± 45^a	267 ± 29^a
pH	7.48 ± 0.35^b	8.03 ± 0.17^a	7.84 ± 0.28^{ab}
Total phosphorus (µg L^{-1})†	63 ± 50^a	22 ± 3^b	61 ± 11^a
Total nitrogen (µg L^{-1})†	525 ± 76^b	504 ± 209^b	717 ± 127^a
DOC (mg L^{-1})†	5.1 ± 0.7^b	2.6 ± 0.2^c	6.7 ± 0.8^a
Suspended solids (mg L^{-1})‡	18.6 ± 4.9^b	3.9 ± 1.5^c	45.8 ± 16.2^a
Colour (A_{440} nm cm^{-1})‡	0.013 ± 0.003^a	0.003 ± 0.001^b	0.021 ± 0.008^a
Planktonic Chl *a* (mg m^{-3})	3.3 ± 1.3^b	1.8 ± 0.6^b	28.8 ± 18.3^a

† measured only in 2000, C. Hudon, unpublished data (n = 11, 7 and 8 for sites 1, 2 and 3 respectively)

‡ measured only in 2001 (n = 3, 4 and 4 for sites 1, 2 and 3 respectively)

Current velocity, temperature and light varied seasonally and between years in the river. Average monthly water level at the nearest gauging station showed a general

Figure 2. Example of seasonal variations in water depth (horizontal marks), water temperature (open circles), macrophyte height (*Vallisneria americana*: white bars, *Potamogeton richardsonii*: hatched bars), light attenuation coefficients (black circles) and in current speed (indicated above the water level mark in cm s^{-1}) measured at site 1 between May and October of 2000.


Water column depth (m)
Water temperature (°C)
Light attenuation coefficient (m-1)
May
Jun
Jul
Aug
Sep
Oct
Nov
14
14
5
9
6
14

decline in water level between June and September of each year and average level values were 0.5 m higher in 2000 (from 4.3 to 4.0 m IGLD85) than in 2001 (from 3.8 to 3.4 m IGLD85). These seasonal and inter-annual differences in water level translated into differences in water depth and light intensity at all sites. In addition, the growth and senescence cycle of macrophytes influenced light attenuation and water velocities within macrophyte stands. In early June, when macrophytes were just emerging from the sediment, light attenuation was caused by turbidity and colour alone and current velocities were relatively high. As the plants grew upwards in the water column, self-shading became, by far, the main light attenuation factor; current velocities decreased considerably and sometimes reached undetectable values, particularly when the macrophytes formed a surface canopy (Figure 2).

Comparison of photosynthetic responses of periphyton and FAM- Filamentous algal mats used light more efficiently than the periphyton, as estimated from P-I relationships acquired for FAM (n = 8) and periphyton (n = 26) between June and September of 2000 and 2001 (Table 2). FAM and periphyton communities showed typical light saturation curves, without photoinhibition for irradiances up to 1000 µmol m^{-2} s^{-1}. P_{max}^{B} (t-test = -2.79, p = 0.009, n = 34) and α^{B} (not significant) were on average higher in FAM than in periphyton. Photosynthetic parameters of FAM were also higher than for periphyton on the four occasions samples were collected from the same site at similar depths (Figure 3), albeit significantly only for α^{B} (paired t-tests = -8.82, p = 0.003, n = 4). Chl *a*-specific dark respiration rates did not differ between FAM and periphyton, either for the entire data set (t-tests = -1.60, p = 0.12, n = 34) or for pairwise comparisons (paired t-test = 0.14, p = 0.90, n = 4). For periphyton, photosynthetic parameters were strongly related to each other, to dark respiration and to biomass whereas these same metabolic descriptors were unrelated for FAM.

Comparison of periphytic metabolic descriptors among sites - Despite varying chemical and physcial characteristics among sites, photosynthetic parameters and dark respiration of periphyton were most strongly related to each other and to biomass. P_{max} and α, were positively correlated for periphyton, whether expressed per unit biomass (r = 0.51, p =

0.008, n = 26) or per unit surface area of substratum (r = 0.74, p < 0.0001, n= 26). Photosynthetic parameters of periphyton were also positively related with dark community respiration (Figure 4). P_{max} and α, expressed per unit biomass, were negatively related to periphyton biomass (Figure 5 - left), whereas biomass-specific dark respiration rates were independent of periphyton biomass on artificial substrata (r = -0.31, p = 0.12, n = 26). Photosynthetic parameters and dark respiration, expressed per unit area, were positively related to periphyton biomass (Figure 5 - right).

The effects of environmental variables on the photosynthetic response of periphyton were relatively small compared to the influence of biomass. Based on stepwise regression models, periphyton biomass had the strongest influence on photosynthetic response and environmental variables (temperature, *in situ* light) were important in explaining additional variation in maximum photosynthetic rate models only (Table 4). Biomass-specific metabolic parameters (α^B/α^A, $I_k{}^B$ and dark respiration) were unrelated to environmental variables (p > 0.05 for correlation coefficients). Saturation PAR and dark respiration rates, expressed per unit area, were positively correlated with temperature (r = 0.61, p < 0.001, r = 0.75, p<0.0001, n=26, respectively). Biomass accounted for the largest part of the explained variation in the maximum rates of gross photosynthesis P_{max}, however, temperature and *in situ* light also influenced P_{max} (Table 3). Periphyton submergence time or development time was positively correlated with epiphyton biomass (r = 0.62, p = 0.0007, n = 26) and unrelated to environmental variables (p > 0.05 for correlation coefficients).

Chemical conditions (e.g. nutrients, DOC) were not measured on each sampling date, so the effects of site were tested using one-way analysis of variance on the residuals of the simple and multiple regression models. No significant differences between sites were observed for α, dark respiration and I_k. P_{max}, however, differed between sites whether expressed per unit biomass (F = 6.99, p = 0.0042, n = 26), or per unit area (F = 13.49, p< 0.0001, n=26) , but differences were relatively small (i.e. mean ± S.E. $P_{max}{}^B$ in mgC mgChl *a* $h^{-1}$of site 1 = 1.1 ± 0.2, site 2 = 1.2 ± 0.2, and site 3 = 1.7 ± 0.4).

Table 2. Summary statistics for photosynthetic parameters, respiration rate, mean sampling depth and light conditions of periphyton and filamentous algal mats (FAM) in Lake St. Pierre. P_{max} is the maximum rate of light-saturated gross photosynthesis, α is the initial slope, I_k is the saturation PAR and R_{com} is the community dark respiration rate calculated per unit biomass (Chl *a*) or per unit surface area of substratum (m^2) for epiphyton. Biomass is measured in mgChl *a* m^{-2} for periphyton and in mgChl *a* m^{-3} for FAM. Light is the *in situ* percentage of surface irradiance at sampling depth calculated from light attenuation coefficients (K).

	Periphyton (n = 26)			Filamentous algal mats (n = 8)		
	Mean	S.D.	Min - Max	Mean	S.D.	Min - Max
<u>per unit biomass</u>						
P_{max}^B (mgC (mgChl a^{-1}) h^{-1})	1.25	0.68	(0.36 - 2.85)	2.16	0.91	(1.28 - 3.52)
α^B (mgC (mgChl a^{-1}) h^{-1}(μmol m^{-2} s^{-1}) $^{-1}$	0.0071	0.0033	(0.0025 - 0.0165)	0.0089	0.0017	(0.0064 - 0.0108)
I_k^B (μmol m^{-2} s^{-1})	196	114	(63 - 570)	253	127	(144 - 472)
R^B_{com} (mgC (mgChl a^{-1}) h^{-1})	0.15	0.10	(0.01-0.35)	0.23	0.16	(0.09 - 0.57)
<u>per unit surface area of substratum</u>						
P_{max}^A (mgC m^{-2} h^{-1})	34.5	20.7	(3.0 - 75.7)			
α^A (mgC m^{-2} h^{-1}(μmol m^{-2} s^{-1}) $^{-1}$)	0.178	0.074	(0.043 - 0.336)			
I_k^A (μmol m^{-2} s^{-1})	195	101	(63 - 433)			
R_{com}^A (mgC m^{-2} h^{-1})	3.8	2.8	(0.42 - 11.8)			
Biomass (mgChl *a* m^{-2} or m^{-3})	38	32	(2.5 - 132)	406	223	(127 - 764)
Mean sampling depth (m)	0.7	0.5	(0.15-1.65)	0.7	0.9	(0.01 - 2.1)
Light (%)	21	16	(1 - 54)	66	42	(11 - 98)

Figure 3. P-I curves for periphyton (black circles) and filamentous algal mats (open circles) from sites 1 and 2 between June and August 2000 and 2001 (date and site are indicated at the top of each graph). Error bars represent ± 1 S.E. of triplicate (2000) or duplicate (2001) samples. The hyperbolic tangent model of Jassby and Platt (1976) was used to fit the data (solid line for periphyton, dotted line for FAM). The dominant genus of filamentous algal mats is indicated for each date.

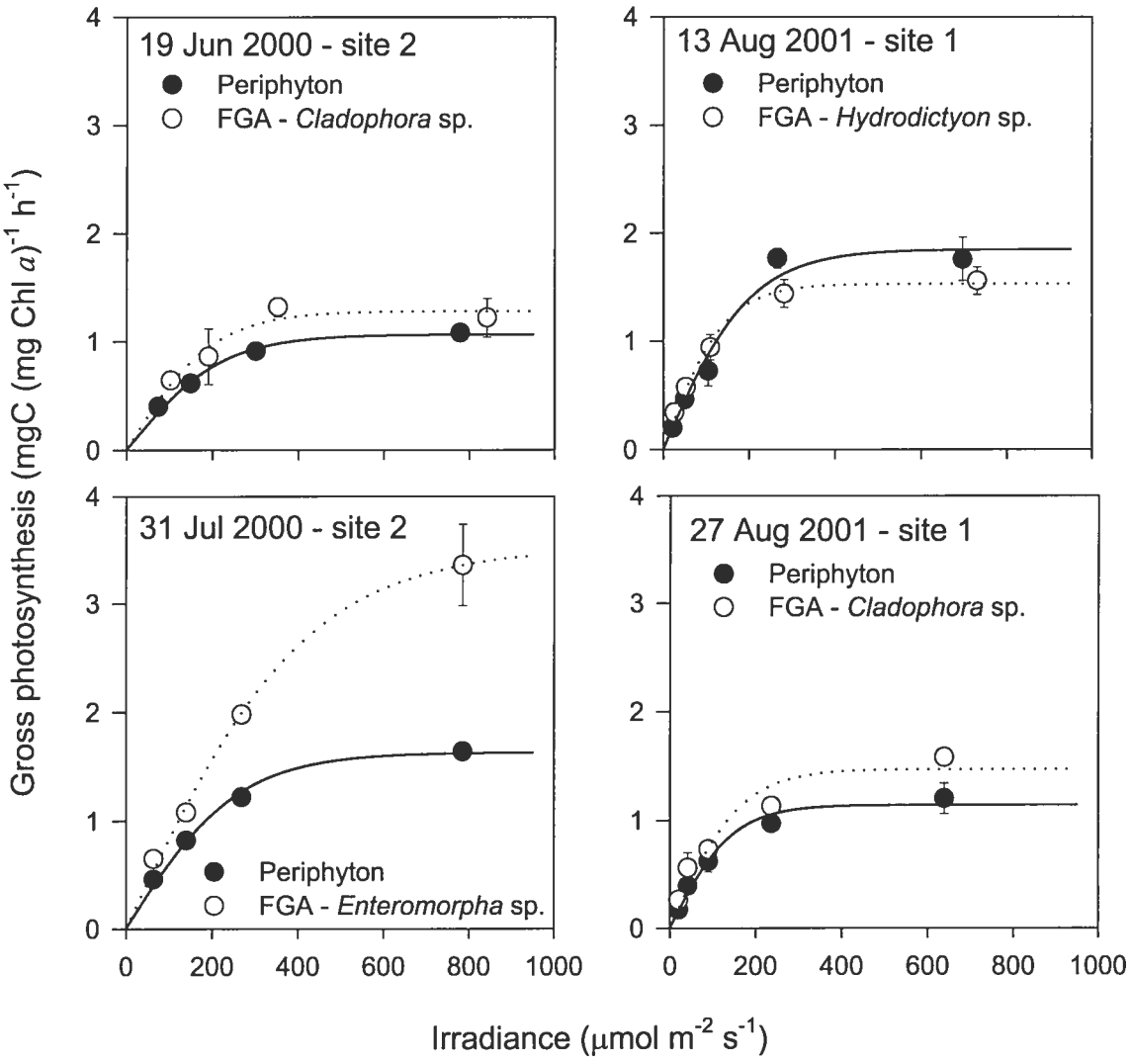

19 Jun 2000 - site 2
Periphyton
FGA - Cladophora sp.
13 Aug 2001 - site 1
Periphyton
FGA - Hydrodictyon sp.
31 Jul 2000 - site 2
Periphyton
FGA - Enteromorpha sp.
27 Aug 2001 - site 1
Periphyton
FGA - Cladophora sp.
Gross photosynthesis (mgC (mg Chl a)-1 h-1)
Irradiance (µmol m-2 s-1)
0
1
2
3
4
0
200
400
600
800
1000

Figure 4. Relationships between periphyton photosynthetic parameters (maximum photosynthesis P_{max}, and initial slope, α) and dark respiration (R_{com}) expressed per unit biomass (left panels) and per unit surface area of substratum (right panels). Data from the various regions of Lake St. Pierre (site 1: black circles, site 2: open triangles, site 3: black squares) and for filamentous algal mats (grey triangles) are shown. Plotted lines were obtained by ordinary least squares regression (n = 26) not including FAM values.

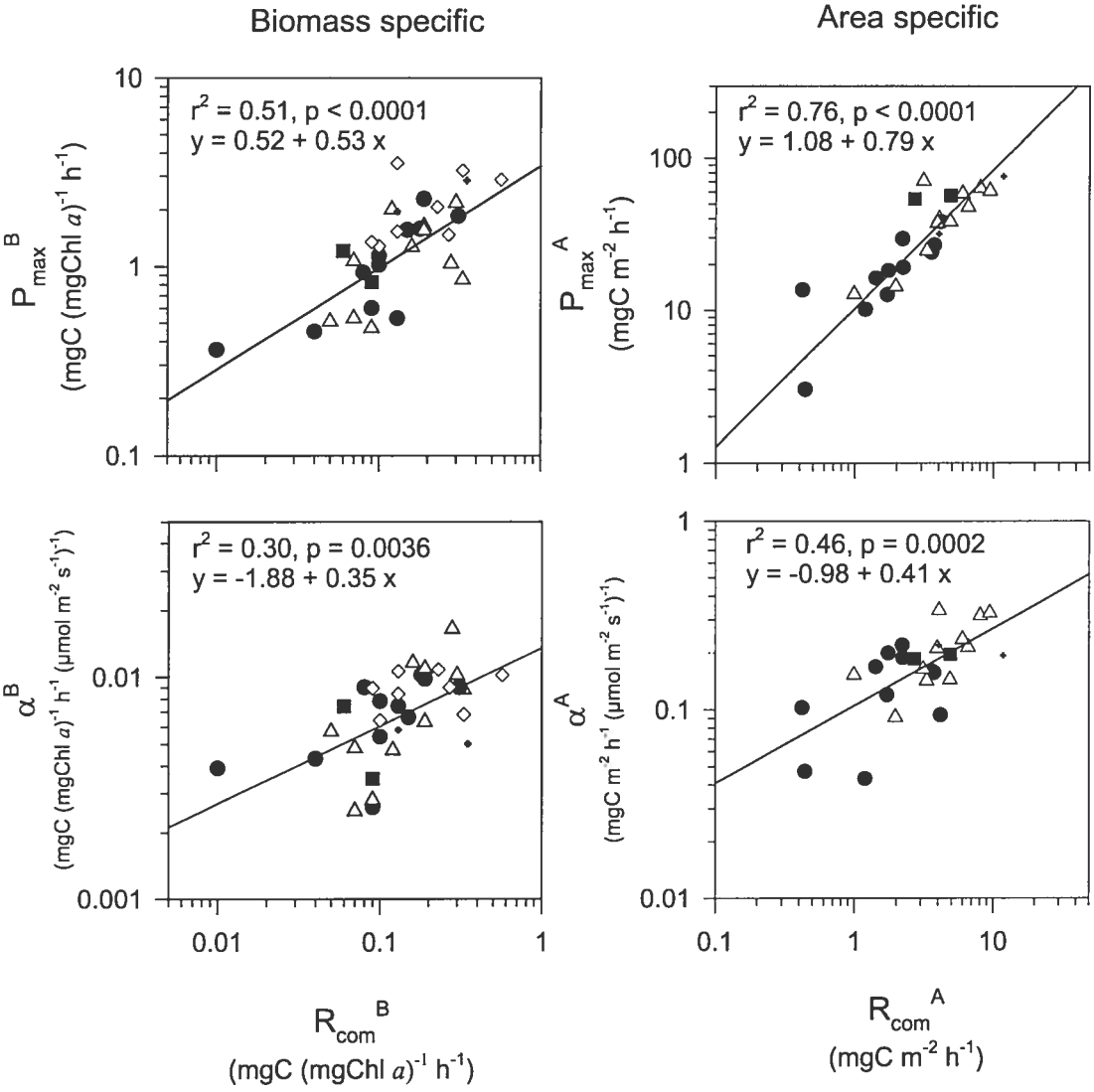

Biomass specific
Area specific
r² = 0.51, p < 0.0001
y = 0.52 + 0.53 x
r² = 0.76, p < 0.0001
y = 1.08 + 0.79 x
r² = 0.30, p = 0.0036
y = -1.88 + 0.35 x
r² = 0.46, p = 0.0002
y = -0.98 + 0.41 x
P max B (mgC (mgChl a)-1 h-1)
P max A (mgC m-2 h-1)
α B (mgC (mgChl a)-1 h-1 (µmol m-2 s-1)-1)
α A (mgC m-2 h-1 (µmol m-2 s-1)-1)
R com B (mgC (mgChl a)-1 h-1)
R com A (mgC m-2 h-1)
10
1
0.1
100
10
1
0.01
0.001
0.01
0.1
1
10

Figure 5. Relationships between periphyton biomass and photosynthetic parameters (maximum photosynthesis, P_{max} and initial slope, α) and dark respiration (R_{com}), expressed either per unit of biomass (left panels) or per unit of surface area of substratum (right panels). Data from the various regions of Lake St. Pierre are shown (site 1: black circles, site 2: open triangles, site 3: black squares). Plotted lines were obtained by ordinary least squares regression (n = 26).

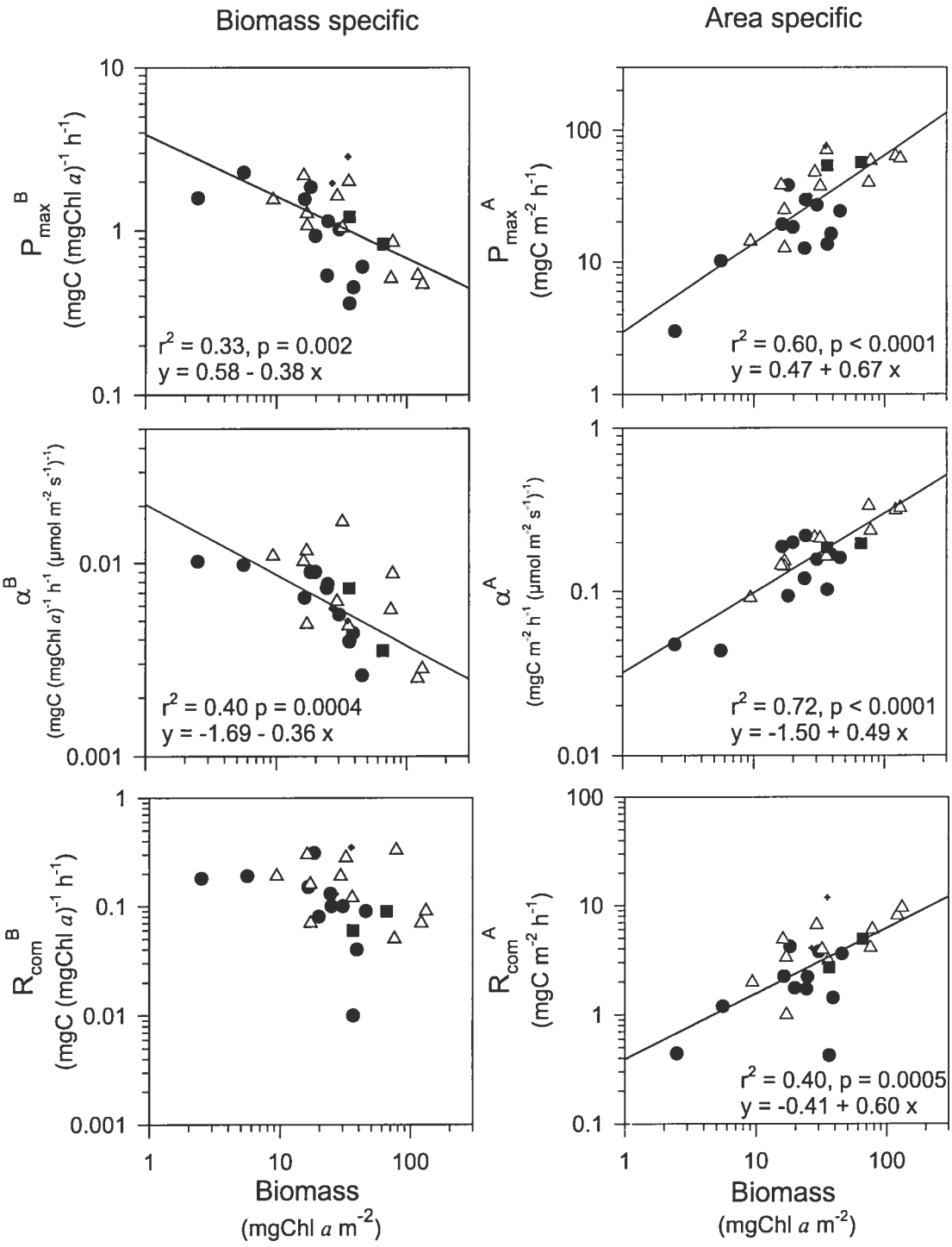

Biomass specific
Area specific
P_{max}^{B} (mgC (mgChl a)$^{-1}$ h^{-1})
P_{max}^{A} (mgC m^{-2} h^{-1})
r^2 = 0.33, p = 0.002
y = 0.58 - 0.38 x
r^2 = 0.60, p < 0.0001
y = 0.47 + 0.67 x
α^{B} (mgC (mgChl a)$^{-1}$ h^{-1} (µmol m^{-2} s^{-1})$^{-1}$)
α^{A} (mgC m^{-2} h^{-1} (µmol m^{-2} s^{-1})$^{-1}$)
r^2 = 0.40 p = 0.0004
y = -1.69 - 0.36 x
r^2 = 0.72, p < 0.0001
y = -1.50 + 0.49 x
R_{com}^{B} (mgC (mgChl a)$^{-1}$ h^{-1})
R_{com}^{A} (mgC m^{-2} h^{-1})
r^2 = 0.40, p = 0.0005
y = -0.41 + 0.60 x
Biomass (mgChl a m^{-2})
Biomass (mgChl a m^{-2})

Table 3. Results of stepwise linear regressions relating $\log_{10}$-transformed maximum photosynthesis rates to environmental factors (*in situ* light, daily PAR and recent irradiance history, temperature) and periphyton biomass (Chl *a,* mg Chl *a* m^{-2}). Abbreviations for environmental factors are: water temperature (Temp, °C) and percentage of incident light at sampling depth (Light, %), calculated as e^{-KZ} from measured light attenuation coefficients (K, m^{-1})) and sampling depth (Z).

Variable	Coefficient	S.E.	*t*	p(*t*)	partial R^2	R^2
$\log_{10} P^B_{max}$ (mgC (mgChl *a*)$^{-1}$ h^{-1}						
intercept	-3.12	1.10	-2.84	0.0093		0.56
$\log_{10}$ Chl *a*	-0.52	0.10	-5.19	<0.0001	0.33	
$\log_{10}$ Temp	2.95	0.87	3.39	0.0025	0.23	
n = 26	S.E.est = 0.17	*F* = 14.43		p (*F*) < 0.0001		
$\log_{10} P^{AREA}_{max}$ (mgC m^{-2} h^{-1})						
intercept	-3.41	0.89	-3.84	0.0009		0.84
$\log_{10}$ Chl *a*	0.64	0.09	6.91	<0.0001	0.60	
$\log_{10}$ Temp	3.12	0.71	4.37	0.0002	0.18	
$\log_{10}$ Light	0.25	0.09	2.93	0.0077	0.06	
n = 26	S.E.est = 0.14	*F* = 39.04		p (*F*) <0.0001		

Depth variations in periphyton photosynthetic parameters - Classical sun-shade adaptation curves were sometimes observed with periphyton collected from deep substrata (low light) showing higher α^B, and lower I_k and P_{max}^B values in comparison with periphyton collected at shallower depths (high light). Such comparisons were made on 5 occasions, when P-I curves were obtained for three top substrata (shallow) and three bottom substrata (deep) collected at a same site (Figure 5). On average, samples from the shallower depth had higher P_{max}^B, I_k, and lower α^B, however, differences were significant only for α^B ($p = 0.05$) and I_k ($p = 0.04$). As a result of strong light attenuation by macrophytes, average light conditions did not always differ greatly between the two depths, with both shallow and deep leaves exposed to low light conditions. The sun-shade response was therefore most apparent when light differed greatly between depths (see, for example the 10 Sep 2001 curve at site 1). Based on the entire data set, maximum biomass-specific photosynthetic rates increased with increasing *in situ* light,

expressed as percentage of surface irradiance ($r^2 = 0.56$, $p < 0.0001$) and decreased with depth, though this relationship was more variable ($r^2 = 0.23$, $p = 0.01$).

Simulation modelling of depth variations in biomass and photosynthetic response of epiphyton on areal daily primary production estimates - Depth variations in epiphyton biomass had a stronger impact on estimates of areal epiphyton production compared to depth variations in photosynthetic response. The effects of both were also strongly dependent on light conditions within the macrophyte stand, and the disparity in estimates between various vertical biomass allocation increased with decreasing light (or increased light attenuation in the water column) (Table 4). When biomass was uniformly distributed (Figure 7 - type A), varying P-I response resulted in small (~ 10 %) changes in production estimates, independent of light attenuation (Table 5). When macrophyte and hence epiphyte biomass was concentrated in the upper part of the water column (Figure 7 – types B and C), assuming a constant distribution of biomass under-estimated areal production, and this error increased with decreasing light and with increasing differences in epiphyte biomass between the top and bottom halves of the stand (type B demonstrated a stronger response compared to type C). When macrophyte and epiphyte biomass were concentrated in the bottom portion of the stand (Figure 7 – type D), error on production estimates resulting from variable photosynthetic response were relatively high (20 to 30 %) regardless of light conditions.

Discussion

Comparison of photosynthetic response of periphyton and filamentous algal mats - Our study shows that filamentous algal mats used light more efficiently than epiphyton. These results are in agreement with previous suppositions that filamentous growth forms, and in particular chlorophytes, are better able to capture light compared to tightly attached forms (Hudon and Bourget 1983; Dodds and Gudder 1992; Hill 1996) and observations of high irradiance thresholds in filamentous green algae (Auer et al. 1983; Turner et al. 1991). As pointed out by Turner et al. (1991), under conditions of increased clarity, FAM have a competitive advantage over tightly attached communities which saturate more quickly in higher light. Fluctuations in water transparency resulting

Figure 6. P-I curves for periphyton from shallow (black circles) and deep (open circles) water depths from sites 1 and 2 between June and September of 2000 and 2001 (date and site are indicated at the top of each graph). Error bars represent ± 1 S.E. of triplicate (2000) or duplicate (2001) samples. The hyperbolic tangent model of Jassby and Platt (1976) was used to fit the data (solid line for shallow samples, dotted line for deep). Average *in situ* light (expressed as the percentage of surface irradiance) at mean sampling depth is indicated .

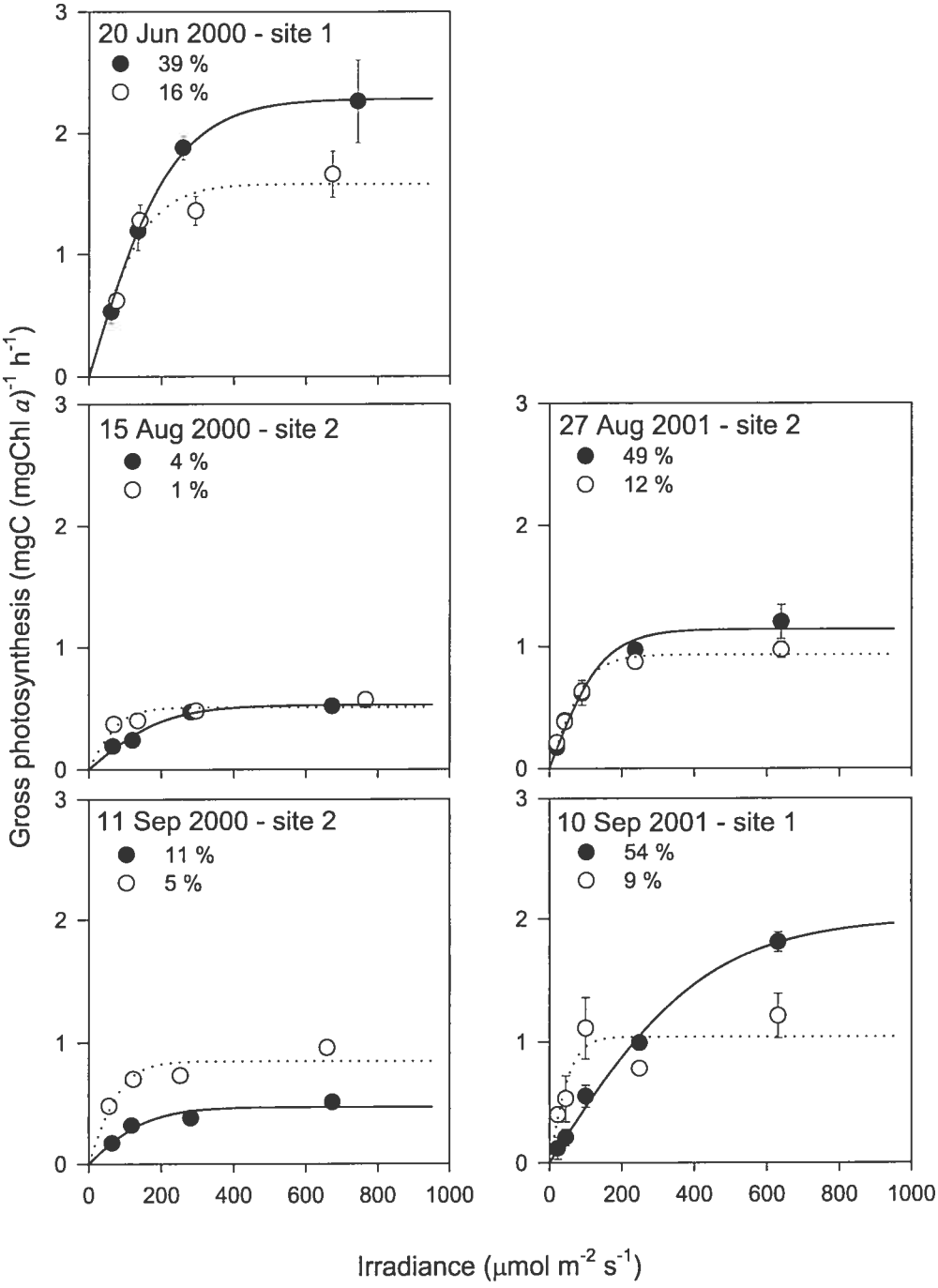
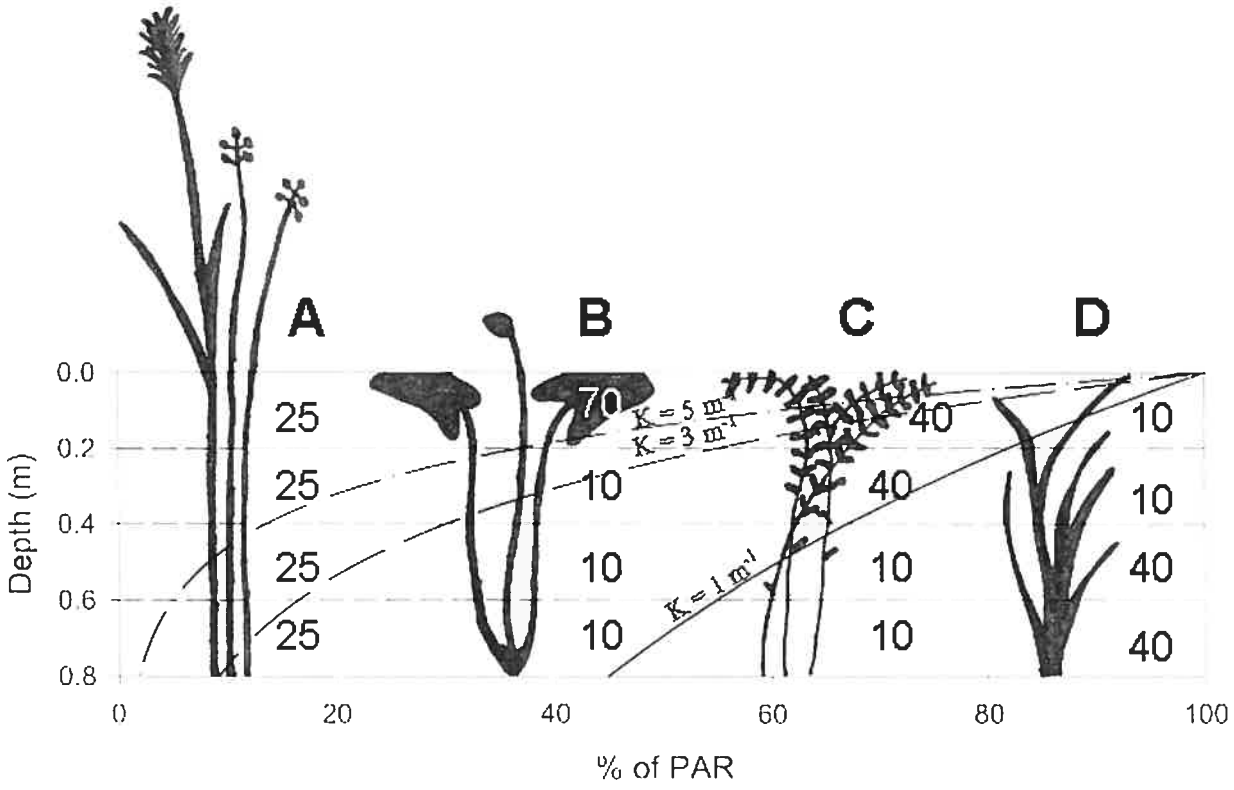

20 Jun 2000 - site 1
39 %
16 %
15 Aug 2000 - site 2
4 %
1 %
27 Aug 2001 - site 2
49 %
12 %
11 Sep 2000 - site 2
11 %
5 %
10 Sep 2001 - site 1
54 %
9 %
Gross photosynthesis (mgC (mgChl a)-1 h-1)
Irradiance (µmol m-2 s-1)
0
1
2
3
0
200
400
600
800
1000

Figure 7. Diagram showing the hypothetical vertical distributions of epiphyton biomass (mgChl *a* m^{-2} (0.2 m depth)$^{-1}$) resulting from differences in the vertical allocation of macrophyte biomass and consequently surface area of substratum for epiphyton colonization within stands of various types and growth forms of aquatic vegetation (A-D). The transmission of light within the water column for different light attenuation coefficients (K in m^{-1}), including the shading effect of macrophyte biomass distribution is also shown.



EMERGENT	FLOATING-LEAVED	SUBMERGED	
i.e. *Scirpus*, *Phragmites*	i.e. *Nuphar*, *Nymphaea*	Canopy-forming i.e. *Myriophyllum*	Rosette-form i.e. *Vallisneria*

Table 4. Areal epiphytic production (mgC m^{-2} d^{-1}) calculated for variable vertical distribution of epiphyton biomass and photosynthetic response in hypothetical macrophyte stands of various types (Figure 7, A-D). Epiphyton biomass (mgChl *a* m^{-2} (0.2m depth)$^{-1}$) is summarised in the table as the ratio of biomass in the top versus bottom 0.2 m stratum of the water column. For each biomass scenario (A-D) depicted in Figure 7, areal epiphytic production was calculated assuming a constant photosynthetic response with depth (P_{max}^{B} = 1.2 mgC (mgChl a^{-1}) h^{-1}, α^{B} = 0.007 mgC (mgChl a^{-1}) h^{-1}(μmol^{-1} m^{-2} s^{-1}) $^{-1}$)), and a variable photosynthetic response in the top versus bottom portion of the stand (P_{max}^{B} - 1.6 : 0.8 mgC (mgChl a^{-1}) h^{-1}, α^{B} - 0.003:0.0011 mgC (mgChl a^{-1}) h^{-1}(μmol^{-1} m^{-2} s^{-1}) $^{-1}$ for different light attenuations in the water column.

Type of vegetation	A		B		C		D	
Biomass (top: bottom)	25 : 25		70 : 10		40 : 10		10 :40	
P-I response with depth	constant	variable	constant	variable	constant	variable	constant	variable
K (m^{-1})								
1	1590	1390	1630	1580	1620	1590	1560	1240
2	1440	1270	1560	1490	1530	1390	1360	1150
3	1240	1120	1470	1390	1410	1230	1060	1010
4	1030	940	1370	1260	1280	1070	780	810
5	860	760	1290	1140	1160	910	570	600

from changing water levels are thus more likely to influence FAM compared to periphyton. Low water levels in Lake St. Pierre during 2001, resulted in a higher occurrence of large masses of filamentous green algal mats compared to 2000, a year with average water levels (C. Vis, unpublished data). Water depth and light conditions are inter-related in rivers (e.g. Cole et al. 1991) and the regulation of river flow in many areas of the world will have important impacts on primary production. The importance of filamentous algal mats to whole-system productivity is difficult to estimate because of their transient nature and their size, which is poorly sampled using methods adapted to periphyton (small surface) or macrophytes. Studies which appropriately quantify their contributions to whole-system production in aquatic systems are required.

Comparison of periphyton photosynthesis from various sites -The reported productivity rates measured using artificial substrata do not represent true productivity rates on natural plants in the St. Lawrence River, as biomass accumulation on natural and artificial substrata were not the same and interactions between the biofilm and its substrata were not measured. Periphyton biomass on natural plants from the same sites were much more variable and depth variations in biomass harder to discern in comparison with artificial substrata. Nonetheless, periphyton photosynthetic parameters and dark respiration rates measured on artificial substrata in this study were comparable with metabolic rates reported in other studies, including studies using natural assemblages (Table 5).

Consistent with the results of broad scale study of all photosynthetic organisms (Enriquez et al. 1996) and previous studies on benthic algae (Boston and Hill 1991; Hill and Boston 1991), we found positive relationships among the photosynthetic parameters (P_{max} and α) both in terms of biomass-specific and areal-specific productivity. Periphyton photosynthetic parameters were also related with dark community respiration, which are less often reported for periphyton. Dark community respiration rates measured on artificial substrata were comparable to areal rates reported for natural periphyton assemblages (Turner et al. 1991; Cardinale et al. 2002), but lower than rates reported by Dodds et al. (1999). Epiphytic assemblages are comprised of autotrophic and heterotrophic organisms, and results from this study indicate metabolic couplings

between autotrophic and heterotrophic processes within the periphyton matrix, consistent with the findings of Neely and Wetzel (1995).

In our study, biomass was the best predictor of photosynthetic response in epiphyton. In agreement with other periphyton studies, we found that biomass-specific photosynthetic parameters decreased with increasing biomass (Marker 1976; Meulemans 1988, Hill and Boston 1991) and areal-specific parameters increased with increasing biomass (Dodds et al. 1999). Reported biomass-specific whole-assemblage photosynthetic parameters demonstrated a similar range of values despite differences in methods, type of ecosystems and community types (substrata) (Table 5). For periphyton, maximum rates of chlorophyll-specific photosynthesis were most commonly under 4 mgC mgChl *a* h^{-1} and at most 8 mgC mgChl *a* h^{-1}, consistent with previous findings of lower ranges of maximum rates of photosynthesis of benthic algae compared to phytoplankton (Krause-Jensen and Sand-Jensen 1998; Morin et al. 1999). We found significant relationship between P_{max}^{B} and biomass and the slope of the log-log relationship (-0.38 ± 0.11) was not significantly different from the slope (-0.22) reported for epiphyton by Goldsborough and Robinson (1996). The relationship between P_{max}^{B} and chlorophyll has also been described as a saturation function, with P_{max}^{B} equal to 0.2 mgC mgChl *a* h^{-1} for chlorophyll concentrations between 100 and 480 mgChl *a* m^{-2} (Müller 1995) or approximately 0.3 mgC mgChl *a* h^{-1} for biomass concentration greater than 250 mgChl *a* m^{-2} (Marker 1976). Although the range in biomass was much narrower in the present study (2 - 130 mg Chl *a* m^{-2}), the lowest value of P_{max}^{B} measured (0.36 mgC mgChl *a* h^{-1} at 130 mgChl *a* m^{-2}) was comparable to the previously reported saturation values. Similar rates of maximum photosynthesis for periphyton biomass greater than 100 mgChl *a* m^{-2} are thus expected.

The initial slope or the light-limited parameter is less reported in the literature despite its importance in estimating periphyton production given the fact that the majority of benthic communities are from low light environments (Hill, 1996). Reported values ranged between 0.001- 0.020 mgC mgChl *a* h^{-1} (μmol m^{-2} s^{-1})$^{-1}$, exhibiting a lower range of values of α compared with phytoplankton (0.002 - 0.036 mgC mgChl *a* h^{-1} (μmol m^{-2} s^{-1})$^{-1}$, Fee 1990). The initial slope was found to vary only

Table 5. Photosynthetic parameters observed in various whole-assemblage periphyton studies. Values indicated means ± SE when reported or ranges in values (minimum and maximum). Abbreviations and units are as follows: maximum gross photosynthesis (P_{max}^B, mgC (mgChl a^{-1}) h^{-1}), initial slope (α^B, mgC (mgChl a^{-1}) h^{-1}(μmol^{-1} m^{-2} s^{-1}) $^{-1}$), saturation parameter (I_k, µmol quanta m^{-2} s^{-1}), and biomass in mgChl *a* per m^2 of substratum.

Study	Type - Location	P_{max}^B	α^B	I_k	Biomass	Remarks
Jones and Adams 1982	Lake - USA	1.0 - 2.6	0.006-0.018	63- 342		Epiphyton on *Myriophyllum* - ^{14}C
Müller 1995	Lake - Germany	0.29 (0.1-3.3)			~1 - 480	Epiphyton on *Phragmites* - ^{14}C
Nozaki 2001†	Lake - Japan	0.1 - 1.2		51 - 206	~ 10 - 1000	Suspensions of epilithon - O_2
Liboriussen and Jeppesen 2003	Lake - Danemark	0.02-0.09				Periphyton on cellulose strips - ^{14}C
		0.26 - 1.5	0.0004 - 0.003		19 - 409	Epipelon - ^{14}C
Robinson et al. 1997	Wetland-Canada	2.4 ± 0.1 (0.1 - 7.9)	0.008 ± 0.001 (<0.001-0.022)	292 ± 17		Periphyton on acrylic rods - ^{14}C
		2.3 ± 0.3 (0.3 - 4.9)	0.006 ± 0.001 (<0.001-0.010)	407 ± 75		Epipelon- ^{14}C
Hill and Boston 1991	Stream-USA	0.55 -2.86	0.003 - 0.011	127 - 292	~ 5 - 140	Periphyton on tiles - ^{14}C
Boston and Hill 1991	Stream-USA	0.26 - 1.4	0.008 - 0.006	98 - 332	23 - 860	Periphyton on tiles or rocks - ^{14}C
Dodds et al. 1999‡	River - New Zealand	1.2 - 3.5	0.003 - 0.020	94 - 834	8-64	Epilithon - rocks in chambers - O_2
This study‡	River-Canada	1.2 ± 0.1 (0.4 - 2.9)	0.007 ± 0.6 (0.003-0.016)	196 ± 22 (63 - 570)	38 ± 6 (2 - 132)	Periphyton on plastic strips - O_2

† The author reported values in carbon units, converted assuming a photosynthetic quotient (P.Q.) equal to 1.
‡ Oxygen units were converted to carbon for the table assuming a P.Q equal to 1.2

with biomass, as expected since light is the predominant variable influencing the relationship between production and irradiance in this portion of the P-I curve, and the accumulation of biomass leads to self-shading within the periphyton matrix (Dodds et al. 1999). In this study, saturation PAR (I_k) was within the range reported in the literature (Table 5) and varied with temperature, reflecting the seasonal changes in light adaptation of the community. Although benthic algae photosynthesis has been shown to correlate with light measured as daily irradiance (Boston and Hill 1991), we found no relationships between daily irradiance or recent irradiance history and photosynthesis. Percent *in situ* light is a better descriptor of the light conditions influencing whole-assemblage epiphytic photosynthetic responses, due to the complicated relationship of light and depth in macrophyte stands, in which shading by macrophytes has a large influence on vertical light distribution.

Inter-related effects of depth and light on epiphyton photosynthetic response - Microscale studies have found evidence of different photosynthetic response at different depths within the periphyton matrix (e.g. Dodds et al. 1999), and acclimation to low light levels has also been observed in stream periphyton (Hill et al. 1995). The classic shade adaptation response, exhibited by phytoplankton and macrophytes from low ambient light environments, is characterised by an increase in photosynthetic efficiency at low light levels (increased α), a decrease in maximum photosynthetic rates at higher light levels and decreased saturation parameters (decreased $P_{max}{}^B$, I_k) (i.e. Richardson et al. 1983). Within a macrophyte stand, strong vertical gradients in light attenuation would be expected to induce shade adaptation in epiphyton communities with depth. We found evidence of shade-adaptation in whole-assemblages of epiphyton from various depths or light levels. In pairwise comparisons, epiphytic communities on artificial substrates located deeper in water column had higher α (2x) and lower saturation PAR (2x) and lower maximum rates of gross photosynthesis compared with leaves from shallower depths. In a study of stream periphyton, $P_{max}{}^B$ increased in shaded communities (Hill et al. 1995), whereas we found increased maximum photosynthetic rates with increasing light, expressed as percentage of surface irradiance. As expected, an inverse relationship was observed between $P_{max}{}^B$ and depth, and although significant, this relationship explained a smaller fraction of the variability in

$P_{max}{}^{B}$ than *in situ* light ($r^2 = 0.23$ compared to $r^2 = 0.56$). The lesser explanatory power of depth in comparison with light likely results from the fact that light intensity at a given depth changes through time, as macrophytes stands grow and progressively occupy the water column.

*Implications for large scale modelling of epiphyton productio*n - Macrophyte stands show marked vertical gradients in biomass and light levels (e.g. Westlake 1964; Titus and Adams 1979). Epiphyton biomass and production have also been shown to vary with depth (e.g. Kairesalo 1983; Meulemans 1988). Despite these findings, areal estimates of epiphyton production are commonly based on single-depth measurements of *in situ* primary production which are extrapolated to daily areal rates based on the diurnal expansion factor. Daily areal rates (per m^2 of substratum) are then extrapolated upwards to total macrophyte surface area (m^2 of macrophyte surface per m^2 of bottom area) available to estimate total daily areal production (per m^2 of littoral zone). Estimates from our study show that areal production may be under or over-estimated by as much as 50% if the vertical distribution of epiphyte biomass and photosynthetic response is not taken into account (see also Hart and Lovvorn 2000). We found that the effects on variations in the vertical distributions of biomass and production are also dependent on light levels, which further cautions against the extrapolation of *in situ* measures of production because of day-to-day variations in light. Since areal production estimates are the basis of whole-system production estimates, errors on estimates caused by not considering depth variations in biomass and light in macrophyte stands are propagated onto estimates of whole-system production. Seasonal variations in light conditions and biomass allocation occurring in macrophyte stands must also be taken into account when scaling-up measures of productivity to estimate annual periphyton production as the variation in biomass between sampling dates and within a site can also have a large impact on the estimation of areal production (Burkholder and Wetzel 1989).

In summary, results of this study demonstrate the importance of seasonal depth variations in biomass and light within macrophyte stands on the estimate of areal epiphyton production. Epiphyton photosynthetic response, similar to other photosynthetic communities, can be modelled as a continuous function of chlorophyll

concentration (Enriquez 1996, Krause-Jensen and Sand-Jensen 1998). A modelling approach based on combining information on macrophyte communities characteristics (growth form, biomass allocation), light attenuation, epiphyton vertical biomass distribution and P-I curve responses of epiphyton would provide a more realistic estimate of large-scale epiphyton productivity in aquatic systems with macrophytes.

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CHAPITRE 4

Primary production by macrophytes, epiphyton and phytoplankton in a large fluvial lake of the St. Lawrence River under different water level conditions

Vis, C., Hudon, C., Carignan, R. and Gagnon, P. Primary production by macrophytes, epiphyton and phytoplankton in a large fluvial lake of the St. Lawrence River under different water level conditions. *Ecological monographs*. In preparation.

ABSTRACT

We examined the primary production by macrophytes, epiphyton and phytoplankton, over a 2-year period with contrasting flow and water levels in Lake St. Pierre, a large (~300 km^2) fluvial lake of the St. Lawrence River (Canada). Spatially-explicit estimates of whole-system production were obtained by combining field and remotely-sensed data and empirical models in a GIS. The relative importance of the various primary producers varied across the range of riverine habitats and spatially within a single habitat. In the wetland habitat which covered ~ 15 % of total surface area, emergent macrophytes contributed roughly half of total macrophyte biomass of the entire lake and algal contributions to wetland production were small (< 20 %). Algal production dominated in the open water habitat (phytoplankton and epiphyton), with smaller contributions by submerged macrophytes (33 to 27 %). Mean annual production at the scale of the lake ranged between 83 and 99 gC m^{-2} yr^{-1}, with emergent macrophyte production ranging from 114 to 129 gC m^{-2} yr^{-1}, submerged macrophyte production from 24 to 25 gC m^{-2} yr^{-1}, epiphyton production from 18 to 16 gC m^{-2} yr^{-1} and phytoplankton production from 28 to 43 gC m^{-2} yr^{-1} between 2000 and 2001, respectively. Plant communities were controlled by different ecological factors: emergent macrophytes were influenced by water levels, submerged macrophytes by exposure to waves and current, epiphyton by the availability of macrophyte substrate and phytoplankton by tributary inputs. A 0.6-m decline in average annual water levels between 2000 and 2001 resulted in a 50 % decrease in the coverage by wetted emergent marsh habitats, a 60 % increase in phytoplankton production in the open water zone, and a 20 % increase in whole-system carbon production (or ~ 5000 mt C). Changes in the relative contributions of primary producers to annual production at the scale of the lake between years were, however, small (< 10 %). GIS-based modeling revealed important spatial variations in primary production which were key to understanding the response of autotrophic production to low water level conditions in this large fluvial lake.

KEYWORDS: Large river, primary producers, GIS modeling, low water levels, relative contributions, phytoplankton, epiphyton, algae, macrophytes

INTRODUCTION

Few studies have quantified whole-system primary production of the various producing communities including macrophytes, periphyton and phytoplankton in large river systems. As primary producers are at the base of the food chain, this lack of information hinders our capacity to understand the flow of carbon to higher trophic levels and to predict the consequences of anthropogenic changes in large rivers. Alteration of flow has been identified as the most serious threat to the ecological integrity of rivers and associated riverine wetlands (e.g. Sparks 1995, Poff et al. 1997, Naiman et al. 2002). Predicting the consequences of altered flow on the functioning of large river systems remains difficult because comprehension of the effects of the complex interactions between flow, physical variables, individual river characteristics and human activities on river processes is limited (Poff et al. 1997, Bunn and Arthington 2002).

In large rivers, autotrophic production is mainly controlled by physical factors, which are in turn linked to hydrology (e.g. Reynolds and Descy 1996). Flow influences many of the environmental characteristics of a river including current speed, water depth, suspended solids and light in the water column, which in turn determine the distribution, abundance and diversity of river organisms (e.g. Poff et al. 1997, Bunn and Arthington 2002). The predominant control of autotrophic productivity by physical factors is also a function of individual river characteristics, such as basin morphometry and flow regime. Human activities on the river, such as damming, dredging and urban and agricultural activities within the drainage basin, further alter physical and chemical river characteristics. The cumulative effects of these variables will determine the primary production of the various plant communities.

In the few studies which have quantified production of all plant communities in large rivers, the importance of the diverse autotrophic producers was highly variable, with phytoplankton production representing 7 - 90 %, periphyton 1 - 15 % and macrophytes 2 - 98 % of total production (Westlake et al. 1980, Lewis et al. 2001, Edwards et al. 1989). As with other aquatic systems, the relative importance of producing communities to total primary production varied with size, depth and nutrient richness of the system (Sand-Jensen and Borum 1991, Wetzel and Ward 1996). In

running waters, increased autotrophy associated with periphyton is reported with increasing stream order up to mid-sized rivers (Minshall et al. 1983, Naiman 1983). In the progression from moderate to large river sizes, increases in turbidity, depth and a greater instability of the substrates result in a shift from attached to suspended primary producers, and large rivers are mainly heterotrophic with low levels of autotrophic production by phytoplankton (Vannote et al. 1981, Minshall et al. 1983, Lewis 1988). Human activities may alter autotrophic production in large rivers. Dams along a river course can increase autotrophic production by reducing flow and turbidity (Ward and Stanford 1983). Increased loading of nutrients through agricultural and urban activity often leads to increased autotrophic production up to a certain point, after which, autotrophic production may decrease due to increased turbidity(Wetzel and Ward 1996). Overall, the models on the functioning of large river systems are mainly theoretical, and there exists few field studies on the primary producers in these large and complex systems.

The size and spatial complexity of large river systems explain in part the lack of overall production estimates in these systems since autotrophic production cannot be quantified by direct field observation alone. Large rivers are often characterized by longitudinal and lateral variations in channel morphometry, and important differences in the physical-chemical characteristics of a river may also arise from tributaries entering the river at various points along its course. Examination of aerial photographs or satellite images of many of the world's largest rivers including the Amazon, the Nile and the St. Lawrence reveals distinct water masses at the confluence of large tributaries, which flow side-by-side over hundreds of kilometers with little or no lateral mixing (.e.g. Nile; Talling and Rzoska 1967, St. Lawrence R.; Hudon 2000). Remote-sensing and geographic information systems (GIS) in combination with empirical models derived from field studies allow for a predictive geographic modeling of these systems (Johnson et al. 1995). To our knowledge, no studies have yet applied these methods to determine the spatial and temporal variability in autotrophic production in a large river.

We report here on the results of a 2-year study on the primary production by macrophytes, epiphyton and phytoplankton in a large fluvial lake of the St. Lawrence River. Field measurements of biomass and productivity were combined with measured

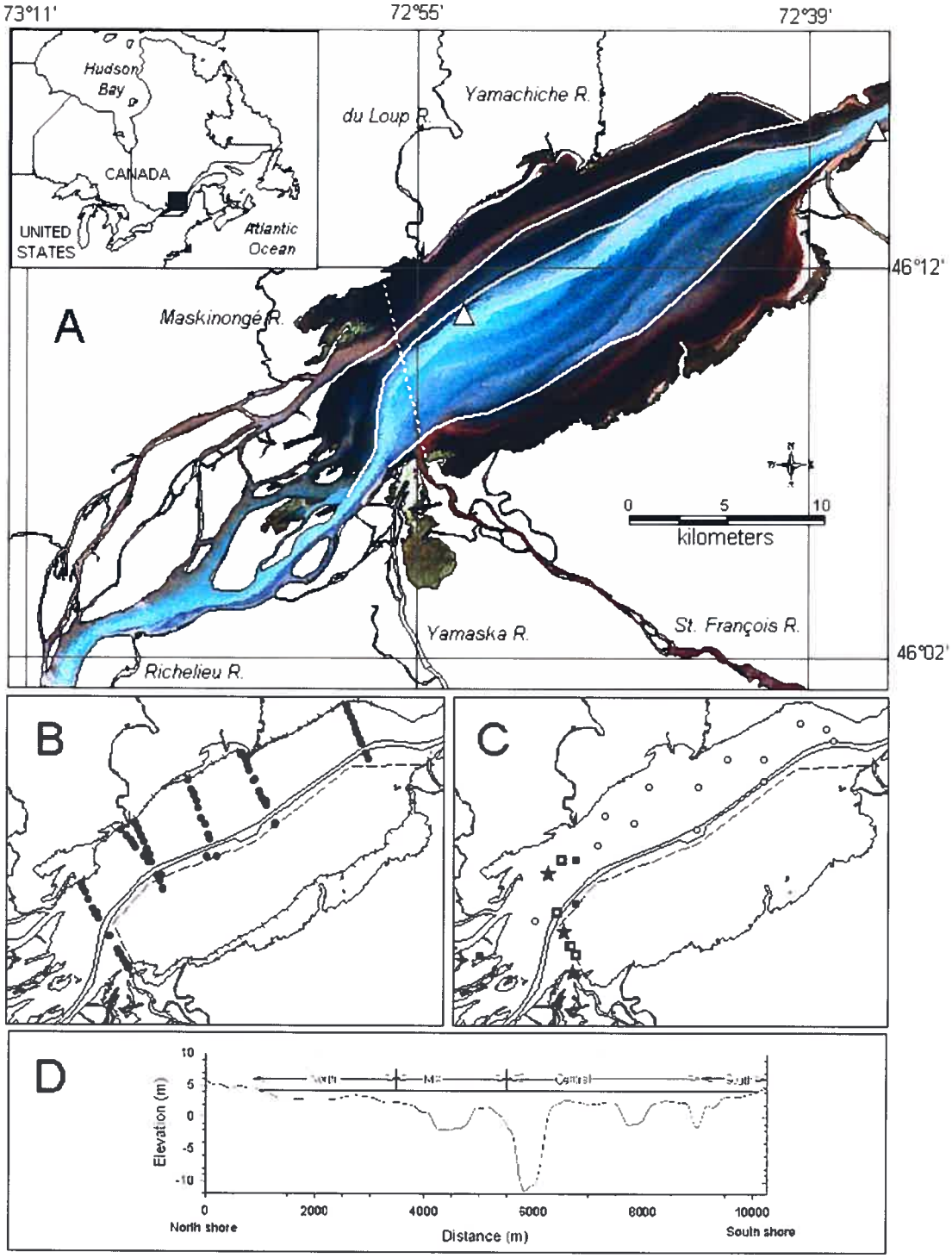
and spatially-derived variables to develop models which predict primary production as a function of environmental variables. Empirical models were then integrated into a GIS to arrive at spatially explicit estimates of macrophyte, epiphyton and phytoplankton production at the scale of the lake (~300 km^2). Finally, we quantified whole-system annual carbon production and the relative contributions of producing communities to total primary production for two years with contrasting water levels.

METHODS

Study site - Lake St. Pierre is an enlargement of the St. Lawrence River, located 100 km downstream of the island of Montreal, Canada (Figure 1A). The large lake (~300 km^2) is relatively slow-flowing (<0.5 m s^{-1}) and shallow (mean depth ~ 3 m) over most of its surface area, with the exception of the fast-flowing (> 0.5 m s^{-1}) and deep (> 12m) main channel which runs through the center of the lake (Figure 1D). Its shallow depth and gentle slopes have favored the expansion of large beds of aquatic vascular plants and the development of riverine wetlands within its floodplain which in turn, support an abundant and highly diversified fauna. The ecological value of Lake St. Pierre has been recognized by its identification as a RAMSAR site (http://www.ramsar.org) and a world Biosphere UNESCO site (http://www.unesco.org/mab/).

Lake St. Pierre is characterized by a large spatial heterogeneity in physical conditions arising from its unique morphometry and hydrology (Figure 1). The relatively shallow lateral areas of the lake are incised by channels of varying depths, including the deep main channel which is maintained by dredging (Figure 1D). Several tributaries, impacted to varying degrees by agriculture, join the river upstream or within Lake St. Pierre. The plume of these rivers flow side-by-side with little lateral mixing, thereby creating a spatially complex system with varying physico-chemical water properties (Figure 1A). Along the north shore flow brown colored waters (DOC concentrations of ~ 5 mg L^{-1}) originating from the Ottawa River. In the central region of the lake flow relatively clear waters originating from the Great Lakes with DOC concentrations of 2-3 mg L^{-1}. A mixture of waters originating from the Richelieu, Yamaska and St. François rivers which are largely influenced by agricultural activity flow along the south shore. These brown colored waters have relatively high

Figure 1. Map of Lake St. Pierre, St. Lawrence River (Canada) and its main tributaries overlying a Landsat TM image (26 August 1986) showing the limits of the 4 main water masses (white lines): the north , mix, central and south (A). Daily water levels were obtained at gauging stations (white triangles) Lake St. Pierre, Curve no2 (upstream, left) and Port St. François (downstream, right). The dotted white line marks the cross-section bathymetric profile presented in panel D. Macrophyte biomass was collected along 5 transects shown in the lower left panel (B) in July and August of 2000 and 2001. The crossed black line indicates the limit of emergent vegetation measured in the field in 2000, the area between this line and the shore was classed as wetland habitat and the area outside of this line was the open water habitat. Phytoplankton and epiphyton sites sampled fortnightly between May and October are shown in the lower right panel (C). Symbols refer to sites sampled in 2000 only (open circles), in 2001 only (full squares), in both years (square with circle), and algal primary production in 2000 and 2001 (black stars). The dotted line indicates the limits of the prohibited zone of the National Defense of Canada (maps B and C).


73°11'
72°55'
72°39'
Hudson Bay
CANADA
UNITED STATES
Atlantic Ocean
du Loup R.
Yamachiche R.
46°12'
A
Maskinongé R.
0
5
10
kilometers
Yamaska R.
St. François R.
46°02'
Richelieu R.
B
C
D
Elevation (m)
10
5
0
-5
-10
North
Mid
Central
South
0
2000
4000
6000
8000
10000
North shore
Distance (m)
South shore

DOC concentrations (5-10 mg L^{-1}) and the highest nutrient concentrations of all water masses in the lake. However, nutrient concentrations are high throughout the lake, with total phosphorus concentrations exceeding 20 µg L^{-1} and total nitrogen exceeding 500 µg L^{-1}.

Field sampling and analytical methods

Hydrological and climate data - Daily water level data for 2000 and 2001 for gauging stations Lake St. Pierre Curve no.2 (02OC016) and St. Lawrence River at Port St. François (02OD002) were obtained from the Marine Environmental Data Services (Department of Fisheries and Oceans of Canada) (Figure 1A). All water level data were referenced to the International Great Lakes Datum of 1985 (IGLD85). Daily flow data for the St. Lawrence River and for various tributaries were obtained from Environment Canada (Richelieu and St. Lawrence R. at Cornwall), Hydro-Quebec (Ottawa R. at Carillon and St. François R.), and from the Ministère Environnement et Faune du Quebec (Yamaska R.). This data allowed us to estimate the flow of the north (Ottawa and Assomption R.), central (St. Lawrence R.) and south (Richelieu, St. François and Yamaska R.) water masses. Daily wind direction and wind velocity data for the St. Hubert weather station (7027320) were obtained from the Meteorological Services of Canada (Environment Canada). We used an average daily PAR of 60 % of the maximum cloudless daily PAR for primary production calculations as this value corresponded to the average daily PAR measured between May and October of 2000 and 2001 (LI 190SA) at our study site.

Macrophytes - Lake St. Pierre was divided into two major habitat categories; wetland habitat, which included various classes of emergent vegetation and the open water habitat with submerged aquatic vegetation (SAV). The limit between wetland (emergent vegetation with > 50% of surface cover) and open water habitats was determined from a hydrofoil field survey (DGPS log) in July of 2000 (Figure 1B). Macrophyte biomass was harvested during the period of maximum biomass (late July to early September) of 2000 and 2001 along five transects located perpendicular to the shoreline (Figure 1B). Transects did not extend over the entire area because access to the southern portion of

the lake is restricted by the Department of National Defence of Canada. Replicate samples (3 to 5) of plant biomass were collected at defined points (DGPS) along each transect. All plant matter (above and belowground structures) was collected in 25 x 25 cm quadrats. In the laboratory, macrophytes were cleaned to remove epiphytes and sediments, identified and separated by species (aboveground only), dried to a constant mass (at 105°C) and weighed. Replicate samples were averaged for each point and expressed in g dry mass per m^2. At each sampling point, water depth and light penetration in open water (LI-COR Quantum sensor LI-190SA and underwater sensor LI-192SA) were measured. The light extinction coefficient (Kwater) was calculated as the slope of the ln-transformed values of light penetration at increasing depth (I_z) divided by surface light intensity (I_o).

Algal biomass - We visited several sites in 2000 and 2001 using a random stratified sampling scheme, stratified by water mass and by broad category of previously determined macrophyte growth-form assemblage (Vis et al. 2003). We sampled 19 sites in 2000 and 10 sites in 2001, fortnightly between May and October of each year (Figure 1C). Each site consisted of a 500 x 500 m quadrat within which a smaller area would be randomly sampled upon each visit to avoid sampling a previously disturbed area within macrophyte stands. We measured total water depth, water temperature, conductivity and pH (Hydrolab Minisonde 4a; Austin, Texas, USA), and water velocity (Marsh-McBirney FloMate model 2000; Frederick, Maryland, USA) 20 cm below the surface. In 2001 only, water samples (1 L) were collected 20 cm below the surface for the determination of suspended solids and color. Suspended solids were determined by filtration (100-800 ml) through pre-combusted, pre-weighed Whatman GF/C filters (pore size 1.2 µm) following the methods outlined in APHA (1998). Color was determined spectrophotometricallly as absorption at 440 nm of filtered water (Whatman GF/C - pore size 1.2 µm) Cuthbert and Del Giorgio 1992. The *in situ* light intensity (PAR) was measured using a surface LI-COR LI-190SA and submersible LI-193SA spherical sensor. At sites with macrophytes, light measurements were made without disturbing the canopy by attaching the underwater light and a pressure sensor to the end of a pole which was lowered obliquely into the macrophyte stand. An average PAR attenuation

coefficient (K_{total}) for the water column (including shading effects by dense macrophytes) was calculated from 3-6 profiles at each site. Previously described macrophyte field data was used to determine the maximum macrophyte biomass at each site.

Phytoplankton biomass, measured as chlorophyll a concentration (mgChla m^{-3}), was determined at each site from water samples (1L) collected 20 cm below the surface. Water samples were filtered (300 - 1000 mL) onto Whatman GF/C filters and frozen until extraction. Epiphyte biomass (mgChla per g dry of $plant^{-1}$), was measured at sites with macrophytes and the habitat characteristics of the macrophytes (species, height in the water column) were recorded. Replicate samples (3-6) of epiphytes on natural plants were collected at a single depth by gently closing a plexiglass cylinder (diameter = 7.6 cm, height =15.2 cm, volume = 695 mL) around the stem of the macrophyte and cutting the protruding ends of the plant. The contents of each box were transferred to a 1 L container and stored in the dark until processing that same day. In the laboratory, the container of epiphytes and plant was shaken by a paint mixer machine for 5 minutes in 2000 and by hand for 1 minute in 2001 to remove epiphytes. Duplicate sub-samples of the suspension were then filtered (Whatman GF/C) and frozen until extraction. For two of the replicates at each site, the quantity of epiphytes remaining on the plant after shaking was determined by cleaning the macrophyte by hand and filtering the slurry of rinsing water. Subsamples of the slurry of epiphytes were filtered (Whatman GF/C filters) and frozen until extraction. When large amounts of filamentous algae were present, these were separated and frozen directly in tubes until extraction. Macrophyte samples were identified to species, dried and weighed. Chla was determined spectrophotometrically following a 24-hour extraction using ethanol 95% and calculated using the equations of Nusch (1980). Epiphyte biomass was calculated as the concentration of Chla (epiphytes on filters corrected for % underestimation + filamentous algae) per gram dry mass of plant.

Although filamentous algae attached to plants were sampled as part of the epiphyton, large masses of algae floating at the surface (metaphyton) were not included in the sampling design, in large part because they were not observed in 2000. In 2001, metaphyton was commonly observed between July and September, and samples were

taken to measure specific-productivity rates (Chapter 3) and to derive relationships between Chla and dry mass. On six occasions in 2001, we measured metaphyton biomass by randomly sampling 3 quadrats (25 x 25 cm) at sites were masses were observed. In the laboratory, the wet weight of each sample was determined and three small subsamples were separated, weighed (wet weight), placed directly in extraction tubes and frozen for Chla analyses. The dry weight of the large sample was determined and the ratio of wet weight:Chla and of dry weight:wet weight were used to derive a Chla:dry weight conversion. Areal biomass was calculated by averaging all quadrats and expressing biomass in g dry m^{-2} and mgChla m^{-2}.

Algal productivity - Phytoplankton photosynthesis was measured in early spring, summer and fall of 2000 and in the early spring of 2001 at three sites (Figure 1C, stars) using methods described in Carignan et al. (1998). Briefly, 40 L of water was collected and triplicate clear and dark BOD bottles were filled, allowing for a two-volume overflow. Bottles were incubated in a five-level, temperature-regulated, rotating wheel incubator at irradiances ranging from ~ 30 to 1000 µmol m^{-2} s^{-1}. After a 4-6 hour incubation, samples were fixed and oxygen concentrations determined from high-precision Winkler titration. Photosynthesis vs irradiance (P-I) curves were then constructed from these data and the computer program PSPARMS (version 4.0, Fee 1990) was used to calculate the maximum rate of light-saturated, biomass-specific gross photosynthesis (P^B_m), initial slope of the P-I curve (α) and saturation PAR (I_k).

Epiphyton photosynthesis was measured at approximately monthly intervals between late June and September of each year using an adapted oxygen method (see Chapter 3 for a more detailed description). We measured epiphyton photosynthesis on artificial substrata at two sites in 2000 and at three sites in 2001 (Figure 1C, stars). Epiphytic photosynthetic parameters (P^B_m, α) were estimated from the fit of the P-I data to the hyperbolic function of Jassby and Platt (1976). For both phytoplankton and epiphyton, mgO_2 were converted to mgC assuming a photosynthetic quotient of 1.2 (Wetzel and Likens 2000).

Description of models and GIS-based modeling

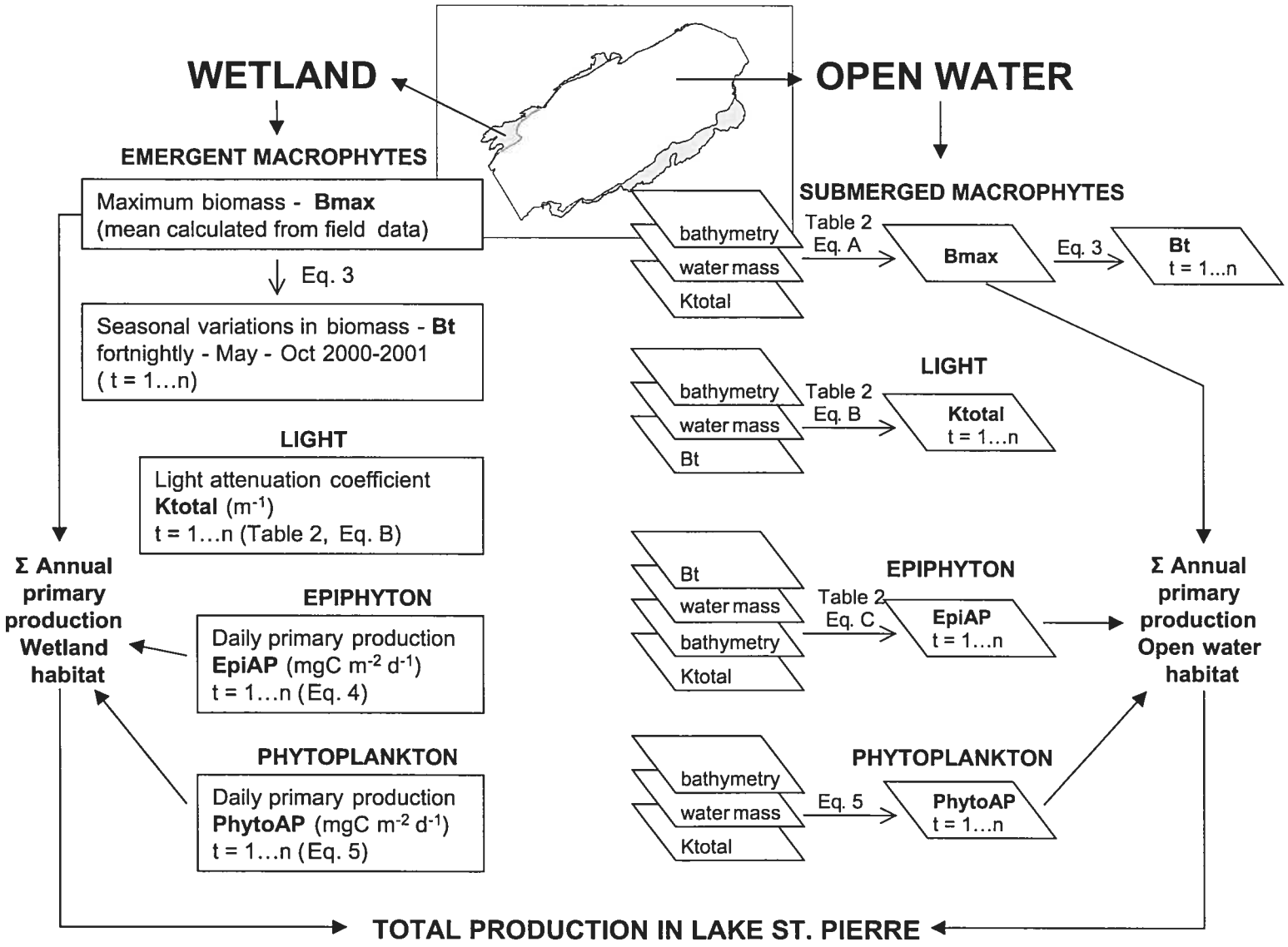
To obtain whole-system estimates of production for each plant community, we developed equations relating physical characteristics to biomass (macrophytes) or

primary production (epiphyton, phytoplankton) from field data collected in 2000 and 2001. We then used these equations and existing empirical models to compute biomass or production within two habitat zones (wetland and open water) in Lake St. Pierre for each year. An overview of the general approach is presented in Figure 2 and each model (equations) will be detailed below. Briefly, spatial data was used to stratify Lake St. Pierre into two major habitats: wetland and open water. In 2000, the wetland habitat zone was underwater during the entire growing season and supported mostly emergent vegetation. Low water levels in 2001 dried out some areas of the lake and resulted in the partial replacement of marshy vegetation (wet) by meadows and mudflats (dry) (Hudon et al. 2004).

Within the wetland zone, production was calculated using mean values of water depth, emergent macrophyte biomass and light for each wetland category (marsh, meadow, mudflat). In the open water habitat, maps of bathymetry, water mass distribution, fetch and generated maps of macrophyte biomass and light attenuation coefficients were combined to calculate spatially-explicit estimates of biomass and production using GIS (continuous). In both habitats, we first determined the maximum areal biomass of macrophytes (Bmax). Next, we modeled the seasonal changes in macrophyte biomass at two-week intervals (Bt) as this information was required to model seasonal changes in light attenuation (K_{total}) and algal production. Derived maps of macrophyte biomass (Bt) and light attenuation coefficients were then used to estimate phytoplankton and epiphyton areal production fortnightly between May and October of each year (symbolized as t = 1…n). Resulting GIS maps were used to calculate total daily and subsequently annual production. Finally, we performed Monte Carlo simulations to approximate the error on estimates of annual production. All GIS-analyses were based on grids with a resolution of 25 x 25 m (pixel size).

Bathymetry - A digital elevation model (DEM) of Lake St. Pierre was constructed by linear interpolation of 85 000 depth soundings referenced to IGLD85 and acquired in 1986 and 1987 by the Canadian Hydrographic Service and in 1999 by Environment Canada. Bathymetric maps were produced for the months of May through October of each year by subtracting the changing surface water elevation and inclination from the

Figure 2. Overview of the methods used to estimate production of each of primary producers within the wetland and open water habitats of Lake St. Pierre. Within the wetland habitat, discrete values determined from field data (macrophyte biomass) or GIS maps (mean depth) were used to calculate production from various empirical models (equations presented in the text or in Table 1). Within the open water habitat, maps of bathymetry, water mass and derived maps were used to calculate spatially-explicit production from empirical models. In both habitats, calculations of seasonal variations in macrophyte biomass (Bt), light attenuation coefficients (K_{total}), epiphyton daily primary production (epiAP) and phytoplankton daily primary production (phytoAP) were made at fortnightly intervals between May and October of each year, represented in the figure as t = 1..n. Total annual production for the entire area was estimated from the sum of wetland (mean areal production x surface) and open water habitats (integration of the surface under the curve of fortnightly values).


WETLAND
OPEN WATER
EMERGENT MACROPHYTES
Maximum biomass - Bmax
(mean calculated from field data)
Eq. 3
Seasonal variations in biomass - Bt
fortnightly - May - Oct 2000-2001
(t = 1...n)
LIGHT
Light attenuation coefficient
Ktotal (m-1)
t = 1...n (Table 2, Eq. B)
EPIPHYTON
Daily primary production
EpiAP (mgC m-2 d-1)
t = 1...n (Eq. 4)
PHYTOPLANKTON
Daily primary production
PhytoAP (mgC m-2 d-1)
t = 1...n (Eq. 5)
Σ Annual primary production Wetland habitat
SUBMERGED MACROPHYTES
bathymetry
water mass
Ktotal
Table 2 Eq. A
Bmax
Eq. 3
Bt t = 1...n
LIGHT
bathymetry
water mass
Bt
Table 2 Eq. B
Ktotal t = 1...n
EPIPHYTON
Bt
water mass
bathymetry
Ktotal
Table 2 Eq. C
EpiAP t = 1...n
PHYTOPLANKTON
bathymetry
water mass
Ktotal
Eq. 5
PhytoAP t = 1...n
Σ Annual primary production Open water habitat
TOTAL PRODUCTION IN LAKE ST. PIERRE

DEM. Surface water elevations were calculated by linear interpolation-extrapolation of daily water levels recorded at Curve no.2 and Port St. François gauging stations (Department of Fisheries and Oceans Canada, Figure 1A).

Water mass distribution - Many of the environmental variables, including Chla, DOC and suspended matter, differ among the various water masses of Lake St. Pierre and water mass, coded as a dummy variable, was included as an independent variable in regression analyses. For GIS-based modeling, the distribution of water masses was delineated from Landsat TM images provided by G. Létourneau, Environment Canada, with water levels similar to the ones used for each modeled period (May, June-October of each year)(Table 1, Figure 4).

Table 1. Landsat TM images used to map the distribution of the four main water masses of Lake St. Pierre in spring (May) and summer (June to October) 2000 and 2001. Daily water level (m, IGLD85) are presented for Lake St. Pierre gauging station Curve no.2 for each image.

Year	2000		2001	
Season	Spring	Summer	Spring	Summer
Date (water level)	4 June 1985 (4.63 m)	13 August 1987 (4.27 m) 21 Sept. 1984 (4.10 m)	27 May 1988 (3.97 m) 8 June 2001 (4.21 m)	11 Aug. 2001 (3.34 m) 21 July 1999 (3.57 m)

Maximum macrophyte biomass (Bmax) - To calculate the maximum aboveground biomass within the wetland habitat, we combined field data from 2000 and 2001 and assigned a mean biomass to each of the 3 wetland classes (discrete value). In the open water zone, previous studies have shown that plants are absent within the main channel and within two smaller channels in the north and south regions of the lake (Fortin et al. 1993) and field quadrats located within these channels were found to have no or a low biomass of SAV. These quadrats were thus excluded from regression analyses data sets and channels were assigned a biomass of 0 g dry m^{-2}in GIS-modeling. In the remainder

of the open water zone, field biomass measurements were combined with environmental variables, which were either measured in the field (light attenuation, water depth), spatially-derived (water mass, coded as a dummy variable and fetch) or calculated (wave effect depth) to develop a multiple regression model predicting maximum SAV biomass. Fetch is a proxy for the effects of exposure to wind, waves and currents, and a fetch grid was calculated in a GIS as the distance in kilometers of open water from the southwest (SW), the predominant wind direction in the St. Lawrence River valley (Hudon et al. 2000). Exposure to wind and waves generate bottom turbulence that rework surficial sediments, and as such, effects of fetch are partly modified by water depth with deeper areas being less influenced. We modeled the relationship between water depth and fetch for wind speeds between 15-28 km h^{-1} as a Michaelis-Menten model using the data presented in Table 4 of Lepage et al. (2000). Based on the non-linear regression fit to the data, the variable wave effect depth (Zw, in m) was calculated as:

$$Zw = \frac{(1.4 \times Fetch)}{(1.8 + Fetch)} \qquad (1)$$

SAV maximum biomass was thus modeled as function of fetch, Zw and a proxy of light effects (water mass and depth) (Table 2, Eq. A). To model SAV biomass over the entire area of Lake St. Pierre, the south water mass was assigned the same dummy coding as the north water mass.

Seasonal changes in macrophyte biomass (Bt)- Macrophytes emerge, grow and senesce between May and October of every year, with important consequences on habitat characteristics (availability of substrate for epiphytic algae) and light conditions, creating shading above (emergent vegetation) and within macrophyte stands. Since field measures of macrophyte biomass and model-derived estimates were representative of maximum biomass only, seasonal changes in biomass were modeled in order to estimate temporal changes in light conditions and algal production. Macrophytes present a barrier to flow, thereby increasing the difference in surface water elevation between the upstream and downstream of Lake St. Pierre (or slope), which is maximal when the

Table 2. Multiple regression models predicting maximum submerged aquatic vegetation SAV biomass (Bmax) in the open water zone, light attenuation coefficients (K_{total}) and epiphyton areal production (epiAP) from environmental variables. Abbreviations are as follows: Zw is the wave effect depth (m), Bt is the seasonal macrophyte biomass (g DM m^{-2}), KZ is optical depth (light attenuation coefficient K (m^{-1}) x water depth (Z)), and I_o is total daily irradiance (mol quanta m^{-2} d^{-1}). Water mass was entered as a dummy variable representing the 3 (macrophyte model) or 4 water masses of Lake St. Pierre[1].

Variable	Coefficient	S.E.	*t*	p(*t*)	partial R^2
A) $\log_{10}$ Bmax - Maximum SAV biomass (g dry m^{-2})					
Constant	1.83	0.15	12.48	<0.0001	
Fetch - SW	-0.035	0.0066	-5.31	<0.0001	0.25
Zw	0.56	0.17	3.42	0.001	0.09
Water1	-0.14	0.054	-2.52	0.014	0.02
Depth	-0.10	0.044	-2.30	0.024	0.02
Water2	0.090	0.049	1.83	0.072	0.03
n = 80, F = 10.12, p(F) < 0.0001, $S.E._{est}$ = 0.27					R^2 = 0.41
B) $\log_{10}$ K_{total} - Light attenuation coefficient (m^{-1})					
Constant	0.20	0.012	16.77	<0.0001	
WaterA	0.11	0.010	11.08	<0.0001	0.31
Bt	0.083	0.012	7.19	<0.0001	0.06
WaterB	0.095	0.017	5.43	<0.0001	0.06
WaterC	-0.031	0.013	-2.40	0.017	0.01
n = 251, F = 2.83, p(F) < 0.0001, $S.E._{est}$ = 0.15					R^2 = 0.44
C) $\log_{10}$ EpiAP - Epiphyton areal productivity ($mgC \cdot m^{-2} \cdot d^{-1}$)					
Constant	0.69	0.39	1.76	0.0832	
Bt	0.0089	0.0022	4.09	0.0001	0.29
WaterC	0.56	0.13	4.19	<0.0001	0.08
-KZ	0.20	0.049	3.98	0.0002	0.06
I_o	0.046	0.013	3.61	0.0005	0.08
WaterB	-0.35	0.14	-2.41	0.0185	0.03
n = 83, F = 18.44, p(F) < 0.0001, $S.E._{est}$ = 0.65					R^2 = 0.54

[1]Dummy variable coding

Water mass	Water1	Water2	Water A	WaterB	WaterC
North	1	0	1	-1	0
Mix	0	1	-1	0	-1
Central	-1	-1	-1	0	1
South			1	1	0

plants reach their maximum standing crop (Boudreau et al. 1994). The growth of plants can therefore be deduced from seasonal variations in slope. Slope is also influenced by tides (Robert et al. 1992) and winds, particularly strong winds with the same orientation as the main axis of the lake (WSW - ENE). We calculated a daily wind effect value (*windWSW*) from climate data in 2000 and 2001 using the following equation:

$$windWSW = \cos(\theta - 67.5)\vec{v}^{\omega} \quad (2)$$

where theta (θ) is the wind direction (in degrees, clockwise from the North) and $\vec{v}^{\omega}$ is the average wind velocity. We then developed a non-linear relationship to model variations in slope as a function of date and wind conditions:

$$\text{Slope (cm/km)} = \frac{U}{2}(Julian - P)^2 + A_a Cos(\frac{2\pi}{\omega} Date - \delta_a) + FwindWSW + M \quad (3)$$

for which the various symbols and parameters are described in Table 3. The non-linear model has three components, a quadratic component to model the effects of macrophyte growth on slope, a cosine component to model the effects of tides and a linear component to model the combined effect of wind and wind direction. The complete model was fitted using non-linear regression to slope data from 2000 and 2001 calculated as the difference in daily mean level between stations Curve no.2 and Port St. François divided by the distance between gauging stations (23 km) (Figure 3, Table 3). The quadratic curve representing the effects of the seasonal growth of macrophytes on slope was then used to calculate the percent of maximum biomass of macrophytes present on various dates before or after the maximum (Julian day 222, or August 9), assuming that macrophytes started to grow on May 21 (based of field observations).

Light - Light attenuation in the water column is the result of a combination of interactions between suspended matter, color, DOC and shading by plants. Based on field data collected in 2000 and 2001, light attenuation coefficients (K_{total}) including the influence of macrophyte canopies on light attenuation were best predicted by water mass

Figure 3. Temporal variations in mean daily slope (cm/km) between upstream and downstream gauging stations of Lake St. Pierre for 2000 and 2001 (circles). The black line is the fitted non-linear model predicting slope as a function of day and wind conditions (Eq. 3, Table 3), and the bold line is the quadratic component of the model which corresponds to the growth cycle of macrophytes in each year (see Table 3).

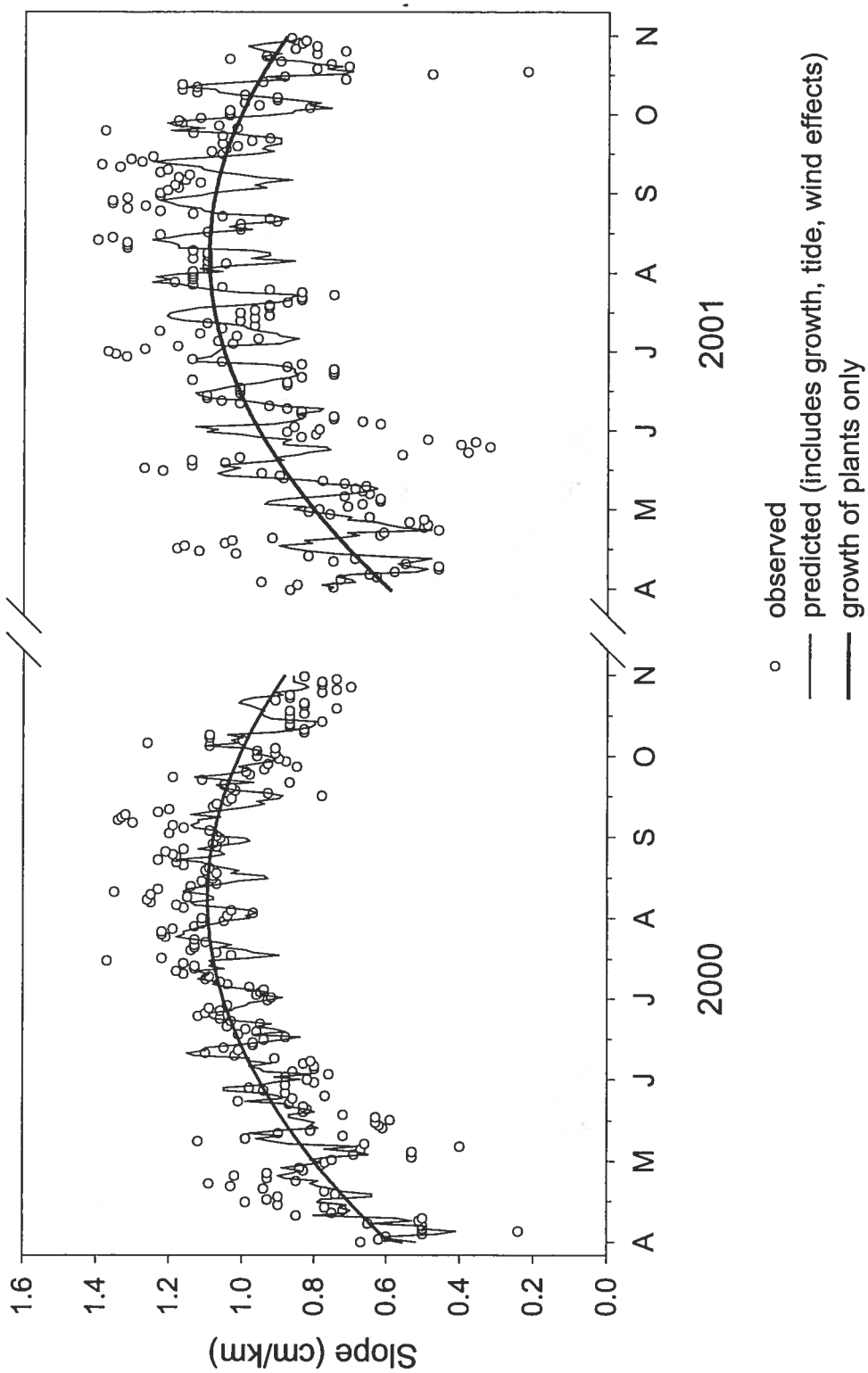

Slope (cm/km)
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
A M J J A S O N
2000
A M J J A S O N
2001
observed
predicted (includes growth, tide, wind effects)
growth of plants only

Table 3. Parameter estimates for the non-linear regression model predicting differences in the surface water elevation between the upstream and downstream of Lake St. Pierre (slope) as a function of day (plant growth and tidal effects) and wind variables. Julian is the Julian day within each year and Date is the number of cumulative days starting from 1 January 2000 (Date = 1). *WindWSW* is a proxy for wind effect combining average wind speed and direction (see Eq.2). The sum of square error (SSE) and number of observations (n) of the model are indicated.

Model: Slope (cm km^{-1}) = $\frac{U}{2}(Julian - P)^2 + A_a Cos(\frac{2\pi}{\omega} Date - \delta_a) + FwindWSW + M$

SSE = 7.83, n = 426

Influence	Parameters	Symbol	Estimate ± Approx. Std Err
Growth of plants	Curvature	U	-0.000067 ± 0.000004
	Day of maximum	P	222 ± 2
	Maximum	M	1.12 ± 0.01
Tide	Period	ω	14.7 ± 0.04
	Amplitude (2000)	A_{2000}	0.078 ± 0.013
	Amplitude (2001)	A_{2001}	0.146 ± 0.023
	Phase (2000)	δ_{2000}	16.61 ± 0.70
	Phase (2001)	δ_{2001}	19.72 ± 1.38
Wind	Wind coefficient	F	0.0047 ± 0.0006

(dummy variable for the 4 water masses) and macrophyte biomass (Table 2, Eq. B). Differences between the brown colored water masses (north and south) and the moderately colored (mix) and clear (central) water masses, represented by the dummy variable WaterA, accounted for the largest part of the variation in light attenuation (70 % of explained variation).

Epiphyton primary production - Daily integrated epiphyton production was calculated for all sites where epiphyte biomass had been measured using the methods outlined by Jones (1984). Similar to the estimation of daily integrated phytoplankton photosynthesis, epiphyton production was calculated by integrating over depth and time measures of 1) the P-I curve 2) the depth distribution of epiphyton biomass 3) irradiance-depth relationship (K_{total}) and 4) diurnal variations in surface irradiance. Average values of photosynthetic parameters were used (P^B_m = 1.25 mgC $mgChla^{-1}$ h^{-1},

α = 0.0071 mgC (mgChla^{-1}) h^{-1} µmol m^{-2} s^{-1}), since seasonal and water mass variations in photosynthetic parameters were either not significant or were relatively small (Chapter 3). At each site on each sampling date, the vertical distribution of macrophyte biomass in the water column by 20-cm depth stratum, was reconstructed on the basis of field observations of plant species composition, height in the water column and of the vertical distribution of macrophyte biomass by species (Annexe III). The vertical distribution of epiphyton biomass (µgChla g dry of plant^{-1}) was variable, and since no clear patterns could be discerned (C.Vis, unpublished data), average epiphyte biomass for each site on each date was multiplied by macrophyte biomass (g dry m^{-2} (20-cm depth)$^{-1}$) to obtain the depth distribution of epiphyton biomass in the water column. Combining the derived data on epiphyton vertical biomass distribution with P-I curves, light extinction coefficients of each site and daily irradiance, daily epiphyton areal production was calculated by numerical integration over depth and time (Daylength, D in hours by 30 minute intervals) as:

$$P_{Zm,T} = \int_0^D \int_0^{Zm} B(z) P_m^B (\tanh \frac{(\alpha - I)}{P_m^B}) dz dt \qquad (4)$$

Integrated daily production could not be calculated directly in a GIS because the information required for such a calculation (plant height and species composition) of SAV was not available for all pixels. Multiple regression analyses showed that 79 % of the total variation in daily production was explained by areal epiphyton biomass. Areal epiphyton biomass and production were both related to seasonal macrophyte biomass, light (optical depth - KZ), and water mass. We modeled epiphyton production directly as a function of macrophyte biomass, light (optical depth and daily irradiance) and water depth (Table 2, Eq. C).

Phytoplankton primary production - Daily phytoplankton production in Lake St. Pierre was estimated using the model of Platt and Sathyendranath (1991):

$$P_{Zm,T} = A\sum_{x=1}^{5}\Omega_x(I_*^m) - A\sum_{x=1}^{5}\Omega_x(I_*^m e^{-KZm})^x \text{ where } A = \frac{BP_m^B D}{K} \quad (5)$$

Where $P_{Zm,T}$ is phytoplankton photosynthesis integrated over depth (Z_m or maximum water depth) and time (T = Daylength), B is phytoplankton biomass (mg Chla m^{-3}), P^B_m, is the maximum rate of biomass-specific photosynthesis (mgC $mgChla^{-1}$ h^{-1}), D is daylength (h), K is light attenuation coefficient (m^{-1}), I^m_* is a normalized irradiance function calculated from surface irradiance at local noon divided by saturation PAR (I_m^0/I_k). Ω_x are coefficients of the polynomial approximations to the analytical solution for $P_{Zm,T}$ (Platt and Sathyendranath 1991).

Phytoplankton photosynthetic parameters varied seasonally in the St. Lawrence River; P^B_m was lowest during cold water periods (spring, fall). We combined our data from Lake St. Pierre with a more extensive data set of phytoplankton productivity in the St. Lawrence River (Blais 2000) acquired using the same methods, to develop regression models predicting photosynthetic parameters (P^B_m and I_k) from water temperature. The following linear regression relationships were used to predict P^B_m and I_k for each date:

$$P^B_m \text{ (mgC mgChla}^{-1}\text{ h}^{-1}\text{)} = -1.7\ (\pm\ 1.2) + 0.39\ (\pm\ 0.07)\ \text{Temp} \quad (6)$$

$$r^2 = 0.59,\ p < 0.0001,\ n = 26$$

$$I_k\ (\mu\text{mol m}^{-2}\text{ s}^{-1}) = -0.15\ (\pm\ 38) + 12.6\ (\pm\ 2.2)\ \text{Temp} \quad (7)$$

$$r^2 = 0.58,\ p < 0.0001,\ n = 26$$

where Temp is water temperature (°C). Since water temperature differs more markedly among dates than between water masses, we used the mean water temperature for the entire lake to calculate photosynthetic parameters for each date. Average phytoplankton biomass (as Chla) was calculated from field data for each water mass on each date.

Metaphyton primary production - We made a first-order estimate of the production by filamentous algal mats in 2001 using the same integration method as for epiphyton

(methods of Jones 1984, Eq. 4). Metaphyton production was calculated between July 30 and September 10 of 2001, using the average biomass measured over that period. Average values of photosynthetic parameters of filamentous algal mats measured in Lake St. Pierre in 2000 and 2001 were used (P^B_m = 2.16 mgC $mgChla^{-1}$ h^{-1}, α = 0.0089 mgC ($mgChla^{-1}$) h^{-1} µmol m^{-2} s^{-1}) (Chapter 3). As no data on the distribution of metaphyton was available, we assumed, based on field observations, that metaphyton covered 10 % of the 0.5 and 1.5 m depth stratum only or 5.3 km^2.

Algal production in the wetland habitat- Algal production and light attenuation in the wetland habitat was estimated using the same methods and assuming the same photosynthetic parameters as for the open water zone. Algal production was assumed to equal zero in the dry meadow and mudflat areas present in 2001 only. Algal production within the wetted marsh areas was calculated on the basis of mean macrophyte biomass and mean water depth (derived from bathymetric maps). Mean phytoplankton biomass (Chla) was calculated as the average for north and south water masses, since wetlands were located only within these water masses.

Epiphyton production was calculated by numerical integration over depth and time for the mean conditions in light, macrophyte biomass and water depth (Eq. 4). The average epiphyte biomass measured on emergent species of macrophytes between May and October in 2000 (C. Hudon, unpublished data) and in 2001 (this study) was used to calculate production on each date. In spring (May), the submerged areas within the wetland zone were assigned a litter biomass of 54 g dry m^{-2} (dead litter from the previous year) based on field measures. We assumed that because the majority of this biomass was flattened with only a small portion out of the water, only 10% would be available as a substrate for epiphytes. Between June and October, the proportion of total emergent macrophyte biomass underwater (available substrate) was calculated from previously developed relationships between the fraction of cumulative biomass and the cumulative length of plants (C. Hudon, unpublished data). We also assumed a uniform distribution of available substrate with depth since the portion of biomass in the water within this zone consisted of the stems of narrow-leaved emergent plants (e.g. *Schoenoplectus*, *Typha*, *Bolboschoenus*). As emergent macrophytes grew, incident light

dropped from 100 % (in May, no emergent plant canopy) to 20 % once the full canopy of emergent vegetation was established (Hudon 2004).

Calculation of total primary production and relative contributions - In the wetland habitat, estimates of daily total production were calculated as mean daily production (algae) or biomass (macrophytes) multiplied by surface area. In the open water habitat, total daily production or biomass equalled the sum of all pixels in individual maps for each date and mean areal production (or biomass) was calculated directly within the GIS (i.e. ArcView). Annual production of macrophytes was estimated assuming that maximum biomass equaled net primary production and that carbon production equaled 46.5% of dry mass (Westlake 1965). Annual production by algal communities was calculated by integrating the area under the curve of seasonal daily production for the ice-free period in Lake St. Pierre (April 1 to December 15). Surface areas of the wetland and open water habitats in Lake St. Pierre were calculated as the weighted mean area in spring (April 1 - May 31, 60 days) and in the remainder of the ice-free period (June 1 to December 15, 197 days).

Error calculations - We used a Monte Carlo simulation approach to calculate approximate errors on total carbon production estimates. For each model, we generated new sets of random parameter values based on their estimation error distribution which took into consideration the covariance between the various parameters (Manly 1998). In the simplest cases, when mean values input into the models were based on field data, we generated random values from the normal distributions based on the error around the mean (the case for temperature and Chla input into phytoplankton model, and maximum macrophyte biomass assigned to each wetland class). We performed 1000 trials, and calculated error from the distribution of generated biomass and production values.

RESULTS

Flow and flow-related variables in 2000 and 2001 - Flow regimes differed markedly between 2000 and 2001, resulting in variations in water level and other flow-related variables in Lake St. Pierre. The timing of the spring maximum differed between years, occurring in late May in 2000 and in mid-April in 2001 (Figure 4). In both years, the

spring peak was driven by increased discharge in the tributaries (north and south water mass), whereas discharge from Lake Ontario did not show strong seasonal difference (central) (Figure 4). During the period of stable flow (summer), water levels were roughly 0.6 m lower in 2001 compared to 2000 and to the 40-year average (1961-2001). Although decreases of 6% to 28% in mean annual flow were observed in all water masses (Table 4), their relative contributions to total flow remained constant between years with the north, central and south water masses contributing approximately 20, 70 and 10 % to total discharge.

The decreased flow in 2001 resulted in a 0.6 m drop in level in the main channel (13.5 to 12.9 m) and a decrease of 22 km^2 or 7 % in the surface area covered by the lake. The mean depth of the lake decreased by a lesser amount (0.4 m), owing to the reduction in total wetted area and basin morphometry (Table 4). When changes in water depth were examined within each water mass, the decrease in mean depth were also less than expected (0-0.2 m) because the surface area occupied by each of the main water masses shifted. In 2001, the area occupied by the central water mass decreased by 34 km^2 or 9 % concurrent with an increase in the area occupied by the south water mass of 22 km^2 or 10 %. With a decrease in flow, water from the Great Lakes preferentially flowed in the main channel and water originating from tributaries expanded their coverage over the lake.

Physical and chemical conditions differed markedly between the various water masses of Lake St. Pierre (Table 5). Conductivity and pH were highest in the central and south water masses, lowest on the north shore and intermediate in the mixed waters. Current speeds were on average moderate (0.16 - 0.34 m s^{-1}), but exhibited large spatial and temporal variations ranging from undetectable in dense macrophyte stands to 1.0 m s^{-1} in the main channel. The colored waters of the north and south were less transparent than the mixed and central water masses and were also characterized by a higher concentrations of suspended solids and nutrients (not shown) and a higher biomass of phytoplankton.

Macrophyte biomass in 2000 and 2001 - Under low water levels, the riverine wetlands occurring at the land - water margin shifted from a predominantly marsh-type habitat to

dry meadow habitat characterized by robust emergent species growing out of the water. In 2000, roughly 15% of Lake St. Pierre consisted of marsh, dominated by narrow-

Figure 4. Average daily surface water elevation at gauging station Curve no.2 (A) and daily discharge of the north (B), central (C) and south (D) water masses of Lake St. Pierre between April and November of 2000 and 2001. Surface water elevations used in the GIS-based modeling are indicated for each date modeled in 2000 (black circles) and 2001 (open circles). The 40-year (1961-2001) average (± 1 S.D.) daily water elevation for station Curve no. 2 is also shown. See Table 4 for complementary information.

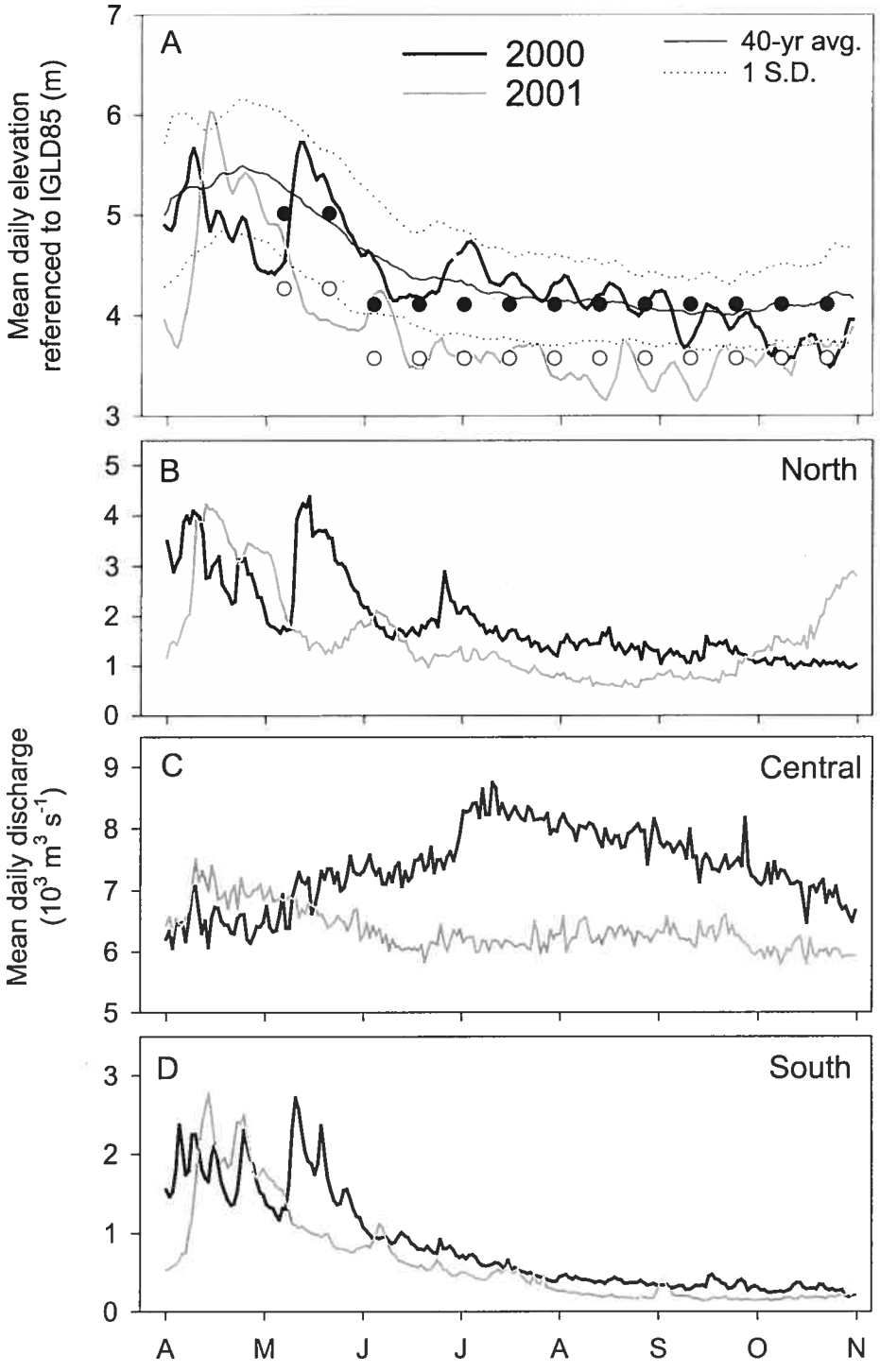

A
2000
2001
40-yr avg.
1 S.D.
Mean daily elevation referenced to IGLD85 (m)
B
North
C
Central
D
South
Mean daily discharge (10^3 m^3 s^{-1})
A
M
J
J
A
S
O
N

Table 4. Summary of annual flow and flow-related variables (surface area and average depth) of the four water masses of Lake St. Pierre for 2000 and 2001.

	Discharge ($m^3 s^{-1}$) Annual mean (range)		Surface area (km^2)		Average depth (m)	
Water mass	2000	2001	2000	2001	2000	2001
North	1881	1771	66	54	1.8	1.6
(Ottawa and Assomption R.)	(645 - 4369)	(558 - 4217)				
Mix			50	52	3.9	3.4
Central	6917	6218	126	92	4.5	4.7
(St. Lawrence R.)	(5369 - 12396)	(5219 - 7509)				
South	776	560	63	85	1.1	1.1
(Richelieu, Yamaska, St. Francois R.)	(187 - 2716)	(132 - 2774)				
Total	9574	8549	305	283	3.2	2.8
	(7386 - 13963)	(6818 - 14039)				

Table 5. Comparison of the mean (S.D.) physical and chemical properties of the four water masses in Lake St. Pierre between 2000 and 2001. The following abbreviations were used; light attenuation coefficient of water column alone (K_{water}), of the water column including shading effects of plants (K_{total}) and Chlorophyll a concentration (Chla),. Paired *t*-tests (by water mass and week) were performed to test the significance of differences between years. n = 10 except for the mix and south water masses in 2000 where n = 8 or 9. Suspended solids and color were only measured in 2001.

Water mass	North		Mix		Central		South		*t*-tests
Major influence	Ottawa River and north shore tributaries				Lake Ontario		Richelieu, Yamaska and St. Francois rivers		
Year	2000	2001	2000	2001	2000	2001	2000	2001	Prob.
Temperature (°C)	18.4	19.0	19.0	19.5	18.3	19.6	18.0	20.3	0.007
	(4.5)	(3.6)	(3.1)	(4.0)	(4.4)	(4.0)	(5.8)	(4.5)	
Current speed ($m\ s^{-1}$)	0.16	0.08	0.27	0.33	0.34	0.29	0.24	0.30	0.33
	(0.05)	(0.06)	(0.05)	(0.8)	(0.16)	(0.06)	(0.12)	(0.07)	
Conductivity ($\mu S\ cm^{-1}$)	170	145	215	155	256	205	229	193	<0.0001
	(25)	(36)	(16)	(41)	(15)	(50)	(35)	(65)	
pH	7.5	7.7	7.7	7.6	8.0	8.2	7.9	8.0	0.26
	(0.1)	(0.7)	(0.2)	(0.3)	(0.2)	(0.3)	(0.2)	(0.3)	
Suspended solids ($mg\ L^{-1}$)		10.4		9.0		6.6		20.7	-
		(4.9)		(2.2)		(2.1)		(9.8)	
Color (A440 nm)		0.011		0.009		0.004		0.013	-
		(0.003)		(0.003)		(0.001)		(0.004)	
K_{water} (m^{-1})	1.7	2.0	1.4	1.6	1.0	1.0	2.6	2.9	0.40
	(0.2)	(0.4)	(0.3)	(0.3)	(0.1)	(0.2)	(1.2)	(1.0)	
K_{total} (m^{-1})	2.1	2.7	1.4	1.6	1.4	1.8	2.8	2.9	0.11
	(0.4)	(1.0)	(0.3)	(0.3)	(0.5)	(0.5)	(1.2)	(1.0)	
Chla ($mg\ m^{-3}$)	2.4	3.3	2.1	3.3	1.9	2.3	11.8	17.2	0.04
	(0.7)	(1.5)	(0.6)	(1.2)	(0.7)	(0.9)	(5.8)	(7.8)	

leaved emergent species (i.e. *Schoenoplectus lacustris*, *S. pungens, Sagittaria latifolia, Eleocharis Smallii* and *Typha augustifolia*) with an average biomass of 270 g dry m^{-2} (Figure 5, Table 6). In 2001, low water levels resulted in the drying out of areas previously covered by marsh which allowed for the additional growth of meadow grass species (i.e. *Phalaris arundinacea, Leersia orysoides*). A small surface (4 km^2) of area previously colonized by SAV was also dried out in 2001, leading to the development of mudflats along the north shore of the lake (Figure 5). Owing to the higher aerial biomass of meadow wetland habitats, the total biomass of macrophytes within the wetland habitat increased by 15 % from 10700 to 12350 mt dry between years. However, the biomass of emergent macrophytes growing in the water decreased two-fold, due to the 50 % reduction in wetted surface area of wetland habitat (Table 6).

In the open water zone, distinct east-west and north-south gradients in submerged macrophyte biomass were found in Lake St. Pierre in both years. In general, SAV decreased from west to east, with increasing fetch, and was higher in the more sheltered south section of the lake than in the north. Submerged macrophytes in the shallowest regions were dominated by a mix of *Potamogeton richardsonii* reaching the surface with an understory of *Vallisneria americana*, whereas deeper regions were characterized by large expanses of *Vallisneria americana* bent with the current. Total open water biomass of SAV varied little between years with decreasing water levels, increasing by less than 5 % (Figure 5, Table 6), owing to a rise in SAV biomass in the shallow regions of the lake. A decrease in SAV biomass at the margins of the central and south water masses between years occurred concurrently with a shift in the distribution of the water masses.

Algal biomass in 2000 and 2001 - Epiphyton biomass, expressed per gram dry mass of plant, was variable with no clear seasonal patterns or interannual differences. Among all sites sampled (2000-2001 combined), epiphyton biomass varied across three orders of magnitudes from 7 to 6605 µgChla g dry $plant^{-1}$ with a median biomass of 412 µgChla g dry $plant^{-1}$. Coefficient of variation between replicates from a single site were high (mean CV = 40 %). Epiphyton biomass was generally highest at sites located in the

Figure 5. Spatial distribution of maximum aboveground dry biomass of aquatic vascular plants in Lake St. Pierre in 2000 and 2001 based on GIS-modeling. Major vegetation classes within wetland habitat are indicated: marsh (wet), meadow and mudflats (dry).

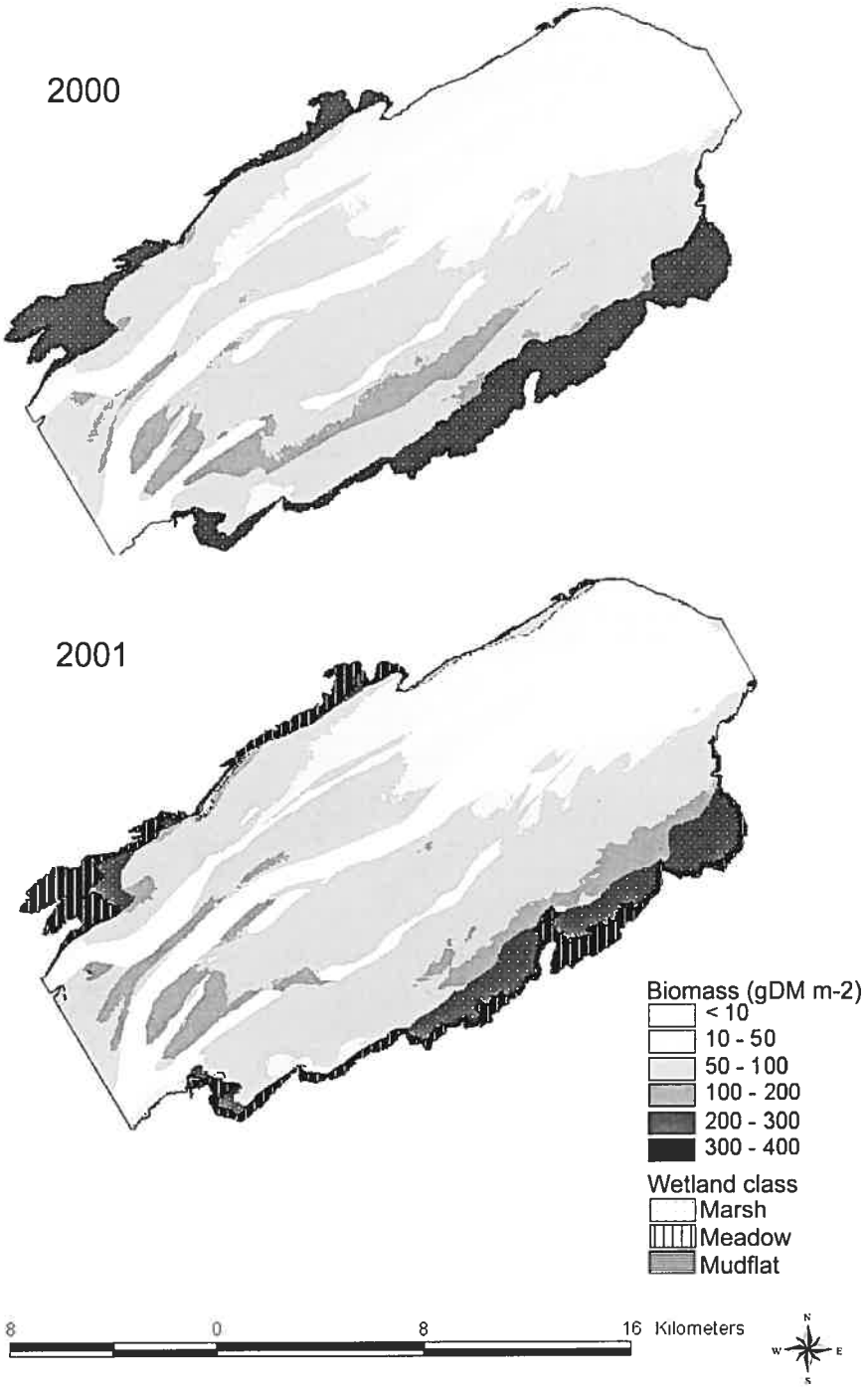

2000
2001
Biomass (gDM m-2)
< 10
10 - 50
50 - 100
100 - 200
200 - 300
300 - 400
Wetland class
Marsh
Meadow
Mudflat
8
0
8
16 Kilometers
N
W
E
S

Table 6. Summary of mean depth (m), surface area (km^2), and maximum aboveground biomass of aquatic vascular vegetation (g dry mass m^{-2}) in Lake St. Pierre in 2000 and 2001. Mean biomass (S.E, n) of wetland classes (marsh, meadow and mudflat) were derived from field measures and all other variables, including mean maximum biomass (min-max) of SAV in open water habitat, were derived from GIS-based modeling. Approximate error on total biomass were calculated from Monte Carlo simulations.

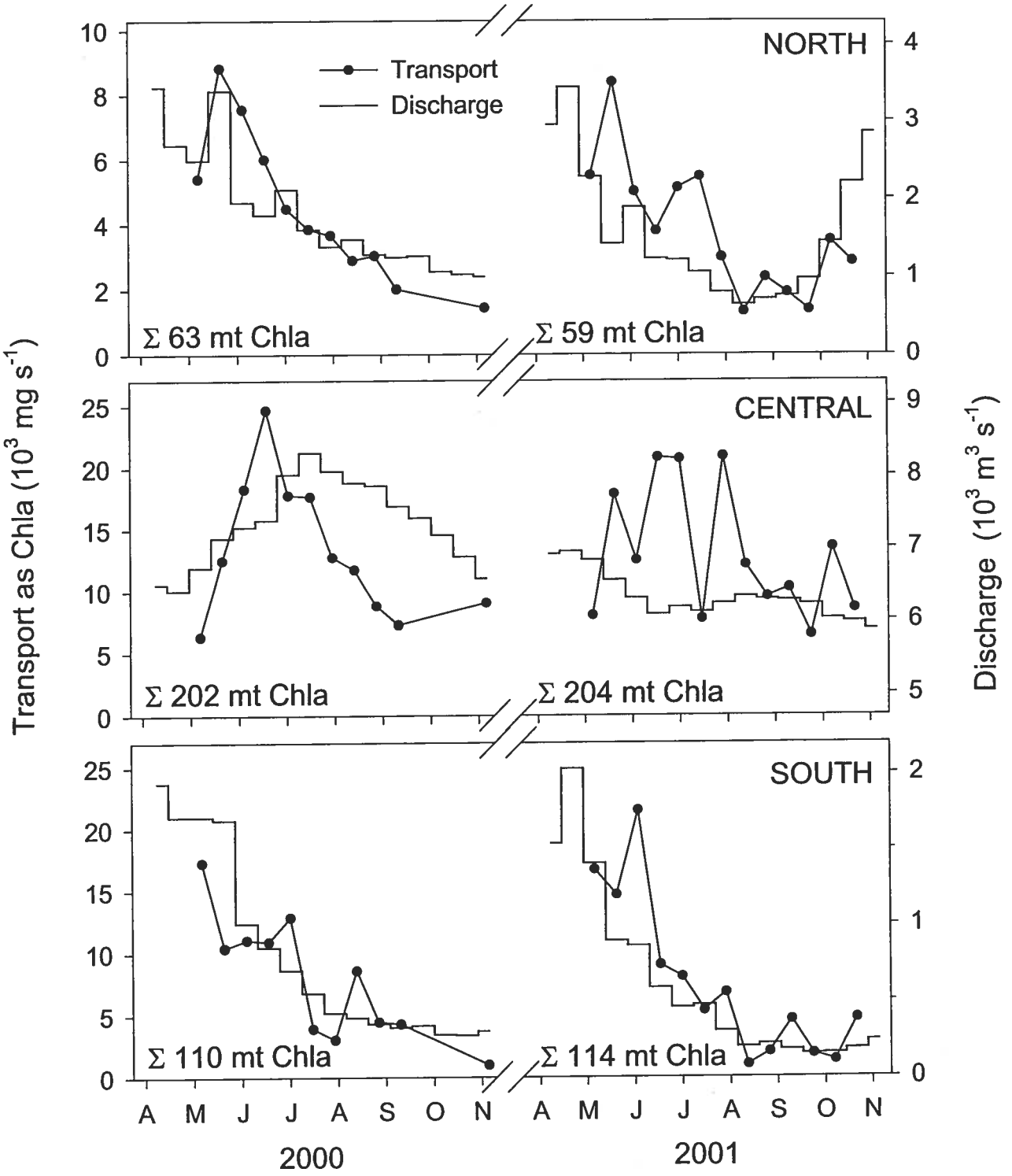
	2000				2001			
			Biomass				Biomass	
Major habitat	Mean depth m	Surface area km^2	Mean g DM m^{-2}	Total (Approx. S. E.) m.t. DM	Mean depth m	Surface area km^2	Mean g DM m^{-2}	Total (Approx. S.E.) m.t. DM
Marsh	0.5	39.6	270 (64, 14)[a]	10700 (2400)	0.2	20.0	270 (64, 14)[a]	5400 (1200)
Meadow					-0.2	19.5	315 (75, 17)[a]	6100 (1400)
Mudflat					-0.2	3.9	220 (127, 3)[a]	850 (500)
Open water	3.4	260.2	52.5 (0 -170)[b]	13700 (1100)	2.9	256.3	54.9 (0 - 190)[b]	14100 (1100)
Total		299.8		24400 (2700)		299.6		26450 (2400)

[a] Standard error and n derived from field measures.
[b] Minimum and maximum range derived from GIS models.

north and central water mass and lowest in the mixed and south water masses. Epiphyton biomass was higher on SAV compared to emergent vegetation from the same marsh sites, with a mean of 1100 μgChla g dry plant^{-1} on SAV compared to 340 μgChla g dry plant^{-1} on emergent vegetation. Based on data from the same sites paired by date, epiphyton biomass averaged 1950 ± 449 (± S.E.) μgChla g dry plant^{-1} in 2000 compared with 1815 ± 407 μgChla g dry plant^{-1} in 2001, although differences between years were not significant ($p = 0.85$, $n = 19$, paired t-test = 0.19). On the basis of lake surface area, epiphyton biomass ranged between 0 and 935 mgChla m^{-2} with a median areal biomass of 38 mgChla m^{-2}.

Phytoplankton biomass was lowest in the central water mass, highest in the south water mass and intermediate in the north and mixed water masses, and increased under low water levels in all water masses (Table 5). In 2000, phytoplankton biomass demonstrated typical seasonal cycles with increasing concentration until June, followed by a decline in concentrations. The exception to this was the south water mass for which no seasonal patterns were discernable (not shown). In contrast, in 2001, under low water level conditions, no seasonal patterns in concentration were observed in any of the water masses. Transport of algal biomass (Chla x discharge) was calculated to examine temporal fluxes in biomass which include the effects of discharge (Lewis 1988). Despite their low contributions to total discharge (< 30 %), tributaries (north and south water masses) contributed half (46 %) of the total flux of phytoplankton biomass compared to the central water mass (Figure 6). In particular, the south water mass represented roughly 10 times less discharge than the central water mass but had a transport of Chla equivalent to half that of the central water mass. In both years, the seasonal transport of biomass in the tributaries paralleled discharge, whereas a different seasonal pattern in transport was apparent in the central water mass. In 2000, a parallel rise of transport and discharge, followed by a decline in algal transport prior to the decline in discharge was observed in the central water mass. This trend is expected for large rivers draining reservoirs or lakes, as algae grown in the lake are flushed with increasing discharge, and the decline in algal transport prior to the decline in discharge is caused by the depletion of algae in the upper water column of the lake (Lewis 1988). Under low flow conditions in 2001, transport of biomass in the central water mass

Figure 6. The transport of algal biomass as Chla between May and November compared with 2-week average discharge by water mass in 2000 and 2001. Total flux (Σ mt Chla) under each curve were calculated over the same sampling period.


NORTH
CENTRAL
SOUTH
Transport
Discharge
Σ 63 mt Chla
Σ 59 mt Chla
Σ 202 mt Chla
Σ 204 mt Chla
Σ 110 mt Chla
Σ 114 mt Chla
Transport as Chla (10^3 mg s^-1)
Discharge (10^3 m^3 s^-1)
A M J J A S O N
2000
2001

showed no apparent links with discharge.

Algal primary production in 2000 and 2001 - Based on specific rates measured in summer, we found that phytoplankton consistently used light more efficiently than epiphyton (Table 7). Maximum rates of gross photosynthesis of phytoplankton were on average 10x higher than those of epiphyton and the initial slope of P-I curve was on average 5x higher. Phytoplankton saturated as higher irradiances, with average I_k = 271 μmol m^{-2} s^{-1} for phytoplankton compared to 171 for epiphyton.

Table 7. Comparison of the biomass-specific photosynthetic and respiration rates of phytoplankton and epiphyton measured simultaneously in June, August and September of 2000 at sites located in the north and central water masses. P^B_m is the maximum rate of light-saturated gross photosynthesis, α is the initial slope of the P-I curve, I_k is the saturation PAR and R_{com} is dark community respiration rates. Volumetric (phytoplankton) and substratum-specific (epiphyton) biomass were measured as Chla. Values are means ± standard error, (minimum and maximum) and n = 6.

.	Phytoplankton	Epiphyton
P^B_m	7.71 ± 1.95	0.86 ± 0.57
(mg C mgChla^{-1} h^{-1})	(5.93 - 9.98)	(0.41 - 1.93)
α	0.0288 ± 0.0052	0.0052 ± 0.0026
(mgC mgChla^{-1} h^{-1} (μmol m^{-2} s^{-1})$^{-1}$)	(0.0200 - 0.0350)	(0.0026 - 0.0100)
I_k	271 ± 54	171 ± 53
(μmol m^{-2} s^{-1})	(213-350)	(99-231)
R_{com}	1.74 ± 1.79	0.11 ± 0.07
(mgC mgChla^{-1} h^{-1})	(0.21 - 4.83)	(0.03-0.21)
Chla	2.3 ± 0.9	51 ± 42
(mg m^{-3} or mg m^{-2})	(1.2 - 3.8)	(4 - 105)

Model-derived estimates of daily areal production demonstrated important seasonal variations in algal production (Figure 7). However, only phytoplankton production varied significantly between years with differing water levels. Within the marsh zone, mean daily algal production was generally low (< 100 mgC m^{-2} d^{-1}) compared to the open water zone (up to 400 mgC m^{-2} d^{-1}). In both the open water and

marsh zones, epiphyton production followed a seasonal pattern similar to that of macrophytes (or availability of substrate) starting off low in the spring and gradually increasing to a maximum in August, followed by a decline in the autumn. Epiphyton mean daily production varied between 10 and 250 mgC m^{-2} d^{-1} and changed little between years. In contrast, mean daily production of phytoplankton varied between 22 and 412 mgC m^{-2} d^{-1} and demonstrated a variable seasonal pattern between years. In 2000, mean phytoplankton production increased from early May to reach a maximum in mid-June, followed by a decrease. In 2001, daily phytoplankton production varied erratically between dates but was always higher than epiphyton production.

Annual primary production of macrophytes, epiphyton and phytoplankton - Model-derived estimates of annual mean production demonstrated important differences in the distribution of production by the three producing communities in Lake St. Pierre across the range of habitats. Macrophyte production was highest in the wetland habitat, and low production was observed over most of the open water area (< 100 mgC m^{-2} d^{-1}). The distribution of macrophyte production changed between 2000 and 2001, with half of the marsh area shifting to dry meadow, resulting in an increase in robust emergent vegetation. Subsequently, algal production in the wetland habitat decreased between years with loss of wetted marsh vegetation.

Within the open water zone, the spatial distribution of algal production varied with community type and between years. Epiphyton production was low over most of the lake (1-100 mgC m^{-2} d^{-1}). Areas with a high biomass of SAV and favorable light conditions were, however, characterized by extremely high levels of epiphyte productivity (> 1000 mgC m^{-2} d^{-1}) (Figure 8). These "hotspots" of epiphyton production increased along the north shore under low water levels and decreased in the southern portion of the lake as a result of shifting distribution of the central (clear) and south (colored) water masses between 2000 and 2001.

Phytoplankton production was highest along the southern section(> 300 mgC m^{-2} d^{-1}) and relatively low over the rest of the lake (100-200 mgC m^{-2} d^{-1}) (Figure 8). Average annual mean production increased under low water levels, from 160 to 235 mgC m^{-2} d^{-1}. This increase was mainly driven by an increase in phytoplankton biomass

Figure 7. Seasonal variations in mean daily areal primary production for phytoplankton and epiphyton in Lake St. Pierre in 2000 and 2001 based on GIS-modeling.

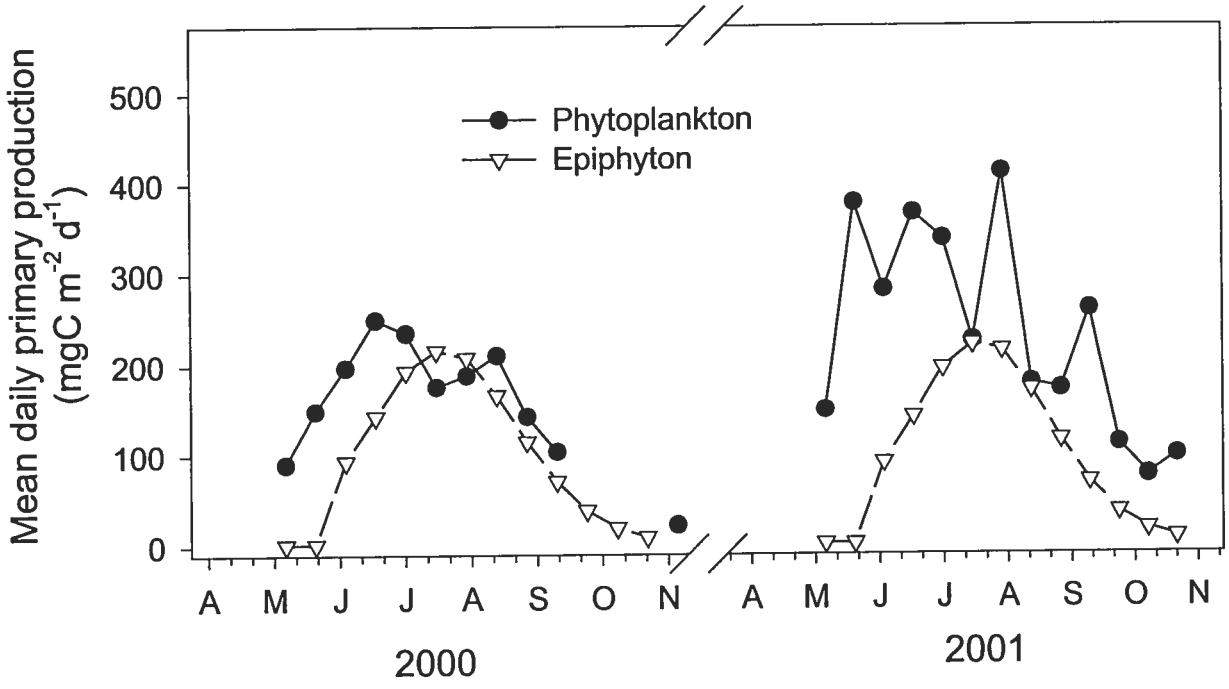
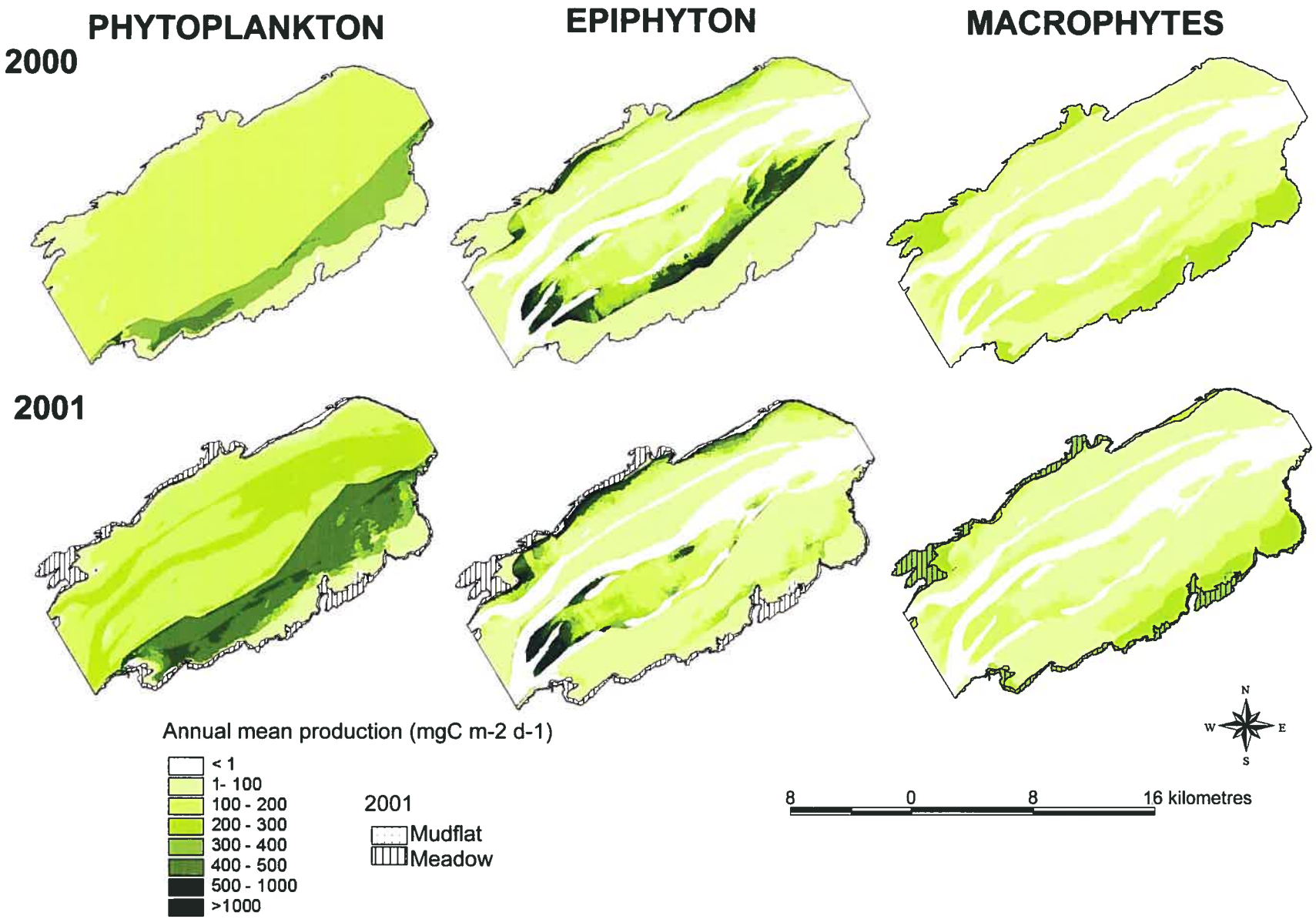

Mean daily primary production
(mgC m-2 d-1)
500
400
300
200
100
0
Phytoplankton
Epiphyton
A M J J A S O N
2000
A M J J A S O N
2001

Figure 8. Annual mean production by phytoplankton, epiphyton and macrophyte communities in Lake St. Pierre in 2000 and 2001, based on GIS modeling.


PHYTOPLANKTON
EPIPHYTON
MACROPHYTES
2000
2001
Annual mean production (mgC m-2 d-1)
< 1
1- 100
100 - 200
200 - 300
300 - 400
400 - 500
500 - 1000
>1000
2001
Mudflat
Meadow
N
W
E
S
8
0
8
16 kilometres

and production in all water masses and by an increase in surface area occupied by the enriched waters originating from the south shore tributaries.

Our data also suggest large increases in metaphyton biomass and production under conditions of low water levels in 2001. Areal biomass averaged 74 g dry m^{-2}, or 250 mgChla m^{-2} and filamentous algal masses were virtual monocultures of green algae, either *Cladophora*, *Hydrodictyon*, *Oedogonium* or to a lesser extent *Spirogyra*. Annual production of metaphyton equalled 1900 mtC yr^{-1} or 6 gC m^{-2} yr^{-1}, equivalent to almost 40% of production by macrophytes or epiphyton (Table 8). Filamentous algae were also separated from vascular plants during the field sampling of macrophytes in 2000 and 2001. Based on the average biomass of all quadrats sampled (entire area), filamentous algal biomass increased significantly between 2000 and 2001, from 0.04 to 1.26 g dry m^{-2} ($p = 0.002$, $n = 39$, test statistic = 74, Wilcoxon Sign Rank).

Table 8. Estimate of the biomass (mean, min-max) and production by filamentous algal mats (metaphyton) in Lake St. Pierre in 2001. n = 19.

	year	2001	
	area	total	wetted
Biomass	g dry m^{-2}	74 (1 - 210)	
	mgChla m^{-2}	250 (16 - 1074)	
Annual	mt C yr^{-1}	1900	1900
Mean annual	gC m^{-2} yr^{-1}	6.2	6.7

Overall, autotrophic production increased under low water levels. However, resulting shifts in the relative contributions of various producing communities to whole-lake production were relatively small (Table 9). Within the wetland habitat, emergent species of macrophytes accounted for half of the total macrophyte production and demonstrated the highest levels of production of any plant community in the lake (~ 100 gC m^{-2} yr^{-1}). Algal production represented 18 - 20% of production within the wetted area of this zone in both years, but drying out of wetland habitats resulted in a decrease

in marsh surface area and in algal production in 2001. Phytoplankton were the dominant producers in the open water zone representing 4j and 53 % of total carbon production in 2000 and 2001, respectively. Epiphyton and macrophytes equally accounted for roughly 5000 - 6500 mt C produced annually in the open water zone. Epiphyton were responsible for 20-26 % of total production and roughly 39 and 27 % of algal production in the open water habitat in 2000 and 2001, respectively. Monte Carlo simulation showed that error on estimates of epiphyton production in the open water zone was much higher (C.V. ~ 70%) than for phytoplankton (C.V. ~37%) and macrophytes (C.V. ~8%).

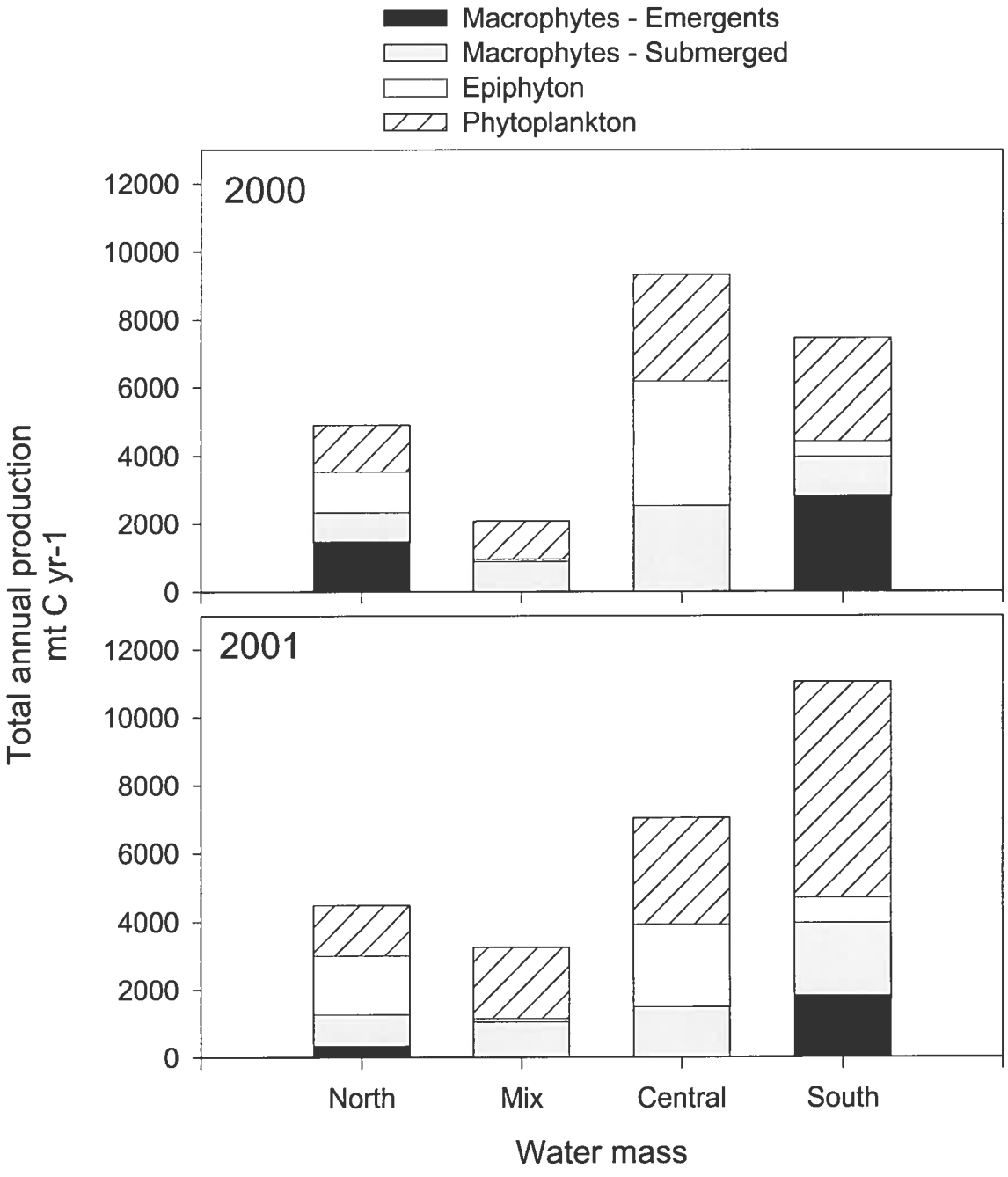
Under low water levels in 2001, annual phytoplankton production in the open water zone increased by 60 % or 18.5 gC m^{-2} yr^{-1}, whereas epiphyton and macrophyte production remained approximately the same (Table 9). Overall, Lake St. Pierre produced 25000 mt C in 2000 and 30000 mtC in 2001, increasing by 20% under low flow and water level conditions. Such an increase was not significant if error on estimates was taken into consideration. At the scale of the lake, macrophytes and phytoplankton were the dominant producers (~40 %) and epiphyton were responsible for roughly 20 % of total production over both years.

Estimates of contributions to total production calculated at the whole-system level masked important differences in the distribution of primary producers within each water mass and between years, as decreases in production in one water mass were cancelled out by increases in another (Figure 9). The north and central water masses were dominated by macrophytes and epiphyton production, with the central water mass having the highest production contribution to total production in 2000. The mixed water mass supported the lowest production of all and was dominated by phytoplankton and macrophyte production. As a result of low submerged macrophyte biomass occurring in relatively deep waters in this area, epiphyton biomass and production were low. Within the central water mass, the main channel was dominated by phytoplankton production whereas the shallow, slow-flowing regions were important areas of macrophytes and epiphyton production. In 2001, the decrease in the coverage of these clear waters over the shoal regions reduced production by macrophytes and epiphyton. In the south water mass, emergent macrophyte production decreased under low water levels and

Table 9. Carbon budget for primary production in Lake St. Pierre for 2000 and 2001. Approximate error on annual production were based on Monte Carlo simulations (presented in brackets).

		Annual ($mt\ C\ yr^{-1}$)			Mean annual ($gC\ m^{-2}\ yr^{-1}$)			Contribution (%)		
	year	**2000**	**2001**		**2000**	**2001**		**2000**	**2001**	
	area	total	total	wet	total	total	wet	total	total	wet
Open water	area (km^2)	261	260	257						
	Phytoplankton	7900 (3000)	12600 (4500)		30.3	48.5	49.0	41	53	53
	Epiphytes	5000 (3900)	4800 (3300)		19.2	18.5	18.7	26	20	20
	Macrophytes	6400 (500)	6500 (500)		24.5	25.0	25.3	33	27	27
	Total	19300 (7900)	23900 (8800)		73,9	91.9	93.0			
Wetland	area (km^2)	44	45	25						
	Phytoplankton	740 (200)	460 (170)		16.8	10.2	18.4	12	7	15
	Epiphytes	380 (120)	150 (40)		8.6	3.3	6.0	6	2	5
	Macrophytes	5000 (1200)	5800 (900)	2500 (570)	113.6	128.9	100.0	82	9*	80
	Total	6120 (1500)	6410 (1250)	3110 (550)	139.1	142.4	124.4			
Total	area (km^2)	305	305	283						
	Phytoplankton	8640 (2600)	13060 (4700)		28.3	42.8	46.1	35	43	48
	Epiphytes	5380 (1600)	4950 (1300)		17.6	16.2	17.5	21	16	18
	Macrophytes	11400 (1300)	12300 (1100)	9000 (800)	37.4	40.3	31.8	45	41	33
	Total	25420 (5800)	30310 (6300)	27010 (5600)	83.3	99.4	95.4			

Figure 9. Relative contributions of the various producing communities (phytoplankton, epiphyton and macrophytes) to annual carbon production in Lake St. Pierre by water mass for 2000 and 2001 (wetted area only).


Macrophytes - Emergents
Macrophytes - Submerged
Epiphyton
Phytoplankton
2000
2001
12000
10000
8000
6000
4000
2000
0
Total annual production
mt C yr-1
North
Mix
Central
South
Water mass

phytoplankton production rose. The south water mass became the area supporting the highest primary production in 2001, largely due to contributions by phytoplankton.

DISCUSSION

Primary production in Lake St. Pierre - The relative importance and magnitude of algal and macrophyte production varied across the range of habitats present in Lake St. Pierre. In the wetland habitat, emergent macrophytes were responsible for the majority of production, with relatively small contributions by algae (~ 20 %). In contrast, the open water habitat was dominated by algal production with lesser contributions by submerged macrophytes. Total production calculated at the scale of the lake was not, however, indicative of the distribution of production by macrophytes and algae within the open water habitat.

The gently sloping shores of Lake St. Pierre support large surfaces of riverine wetlands which occupy ~ 15 % of the total surface area but are responsible for half of the overall macrophyte biomass in Lake St. Pierre. Despite being the area with the highest level of production in the lake, annual production by emergent vegetation in Lake St. Pierre was on average low (120 gC m^{-2} yr^{-1}) compared to emergents from other temperate river communities (320 - 3700 gC m^{-2} yr^{-1} - Wetzel 2001). Low production may have been due to a predominance of quadrats from the exposed north shore of the lake in which scattered emergents dominated (i.e. *Scirpus*, 60% of biomass) with a lesser presence of dense, more robust emergent species (*Typha* and *Sagittaria* < 35 % of biomass). Our estimates are also likely conservative because we measured biomass once during the period of maximum growth, thereby underestimating net annual aerial production (Dickerman et al. 1986) and we did include belowground biomass in our estimate of production, which is relatively high for emergent vegetation (Wetzel 2001).

Algal production contributed to < 20 % of total production in the wetland zone, with epiphyton making only small (< 7 %) contributions to total carbon fixation in comparison to emergent macrophytes. Algae were also found to contribute little to total production in floodplain lakes (< 2 % - Lewis et al. 2001) and in wetlands (< 10 % - Stanley et al. 2003). The low contributions by algae to carbon production are in contrast with previous wetland studies (e.g. Hooper and Robinson 1976) and conceptual models

(Goldsborough and Robinson 1996) that have found algae to be the major contributors to wetland primary production. Model-derived estimates of wetland production from this study must, however, be interpreted with caution because calculations were made on the basis of mean values of biological (biomass) and physical (water depth, light) data applied to a large area (40 km^2). In particular, emergent macrophyte biomass was derived from little field data that did not include the more sheltered sites along the south shore and variation between quadrats was large (C.V. between 70-98 % for the various wetland classes). A more comprehensive study of production of macrophytes and algae within Lake St. Pierre's riverine wetlands is required, in particular because this was the area most affected by low water levels.

Within the open water habitat, the relative importance of macrophyte, epiphyton and phytoplankton production demonstrated important spatial and temporal variations which were largely explained by the unique physical features of Lake St. Pierre. Shallow water depths in the open water habitat offset the negative impacts of turbidity ($K > 1\ m^{-1}$) on light conditions within Lake St. Pierre. Bottom light intensities were greater than 1%, thus favoring the development of SAV biomass throughout the lake, which in turn supported a high biomass and production by epiphytes. The range in submerged macrophyte biomass (0-190 g dry m^{-2}) was comparable with other sites in the St. Lawrence R. (Hudon 1997) and other temperate rivers (e.g. Chambers et al. 1991, French and Chambers 1997). Although our estimate of annual production is conservative because it is based on maximum biomass only, annual production of SAV (mean ~25 gC m^{-2} yr^{-1}) was, however, low compared to other submerged macrophyte communities from temperate rivers (8 - 400 gC m^{-2} yr^{-1} - Wetzel 2001), likely due to the effects of turbidity and currents. Most of the lake is exposed to wind, waves and current, and these factors associated with extensive fetch in shallow waters play a major role in determining the distribution and biomass of SAV in Lake St. Pierre. Other studies on submerged macrophytes have also found fetch, current and water depth to be play a key role in the distribution and biomass of submerged plants (e.g. French and Chambers 1997, Rea et al. 1998, Hudon et al. 2000, Lougheed et al. 2001). Submerged macrophytes in Lake St. Pierre were predominantly *Vallisneria americana*, a species

well-adapted to current, further supporting the argument that current and fetch limited SAV biomass in this system.

The temporal and spatial dynamics of SAV in turn influenced epiphytes, as epiphyton biomass and production were directly related to the availability of substrate and its position in the water column. Similar to measurements of epilithon in rivers (e.g. Morin and Cattaneo 1992, Chételat et al. 1999) and of epiphyton in lakes (e.g. Cattaneo and Kalff 1980, Lalonde and Downing 1991), epiphyton biomass and production in the Lake St. Pierre varied over 2 -3 orders of magnitude. Variations in areal biomass and production were highly dynamic both in time and in space, as the surface area available for colonization demonstrated strong seasonal cycles and large spatial variations in the open water habitat. Relative contribution of epiphyton to total production is largely a function of surface area available for colonization (Allen 1971, Kowalczewski 1975), and based on mean SAV biomass, average surface area for colonization by epiphyton in Lake St. Pierre was 5 m^2 m^{-2} of lake bottom during the period of maximum macrophyte biomass (roughly one month). Important spatial and temporal variations in epiphyton production were observed, with some areas having very high values of available surface area for colonization (17 m^2 m^{-2}) and during the maximum biomass of macrophytes, mean daily epiphyton production equalled that of phytoplankton in the open water habitat. Seasonal cycles in macrophyte and epiphyton production reduced, however, their relative contributions to annual production, as these plants were present during only 5 months of the year (end of May to October) compared to phytoplankton which was present over the entire ice-free period. The effects of the timing and spatial distribution of production likely influence relative contributions of algal production in river food webs.

Error on epiphyton production in the open water was high (CV ~ 70%), and GIS-derived estimates in the present study did not consider vertical variations in light and the distribution of biomass within macrophyte stands, which can be important determinants of epiphyton production (Hart and Lovvorn 2000). Integration of primary productivity directly within a GIS would yield more accurate estimates of epiphyton areal production, although, such an estimate would require information of the SAV species composition and height over the entire lake. Notwithstanding these limitations, annual rates of

epiphyton production were found to be lower in wetlands (3-9 gC m^{-2} yr^{-1}) compared to open water habitat (19 gC m^{-2} yr^{-1}). Similar to the littoral zones of lakes (summary in Wetzel 2001), annual epiphyton production equalled that of macrophytes in the open water habitat. Overall, epiphyton contributed to 30-40% of carbon production in the open water, indicating that it could be an important food source for secondary producers.

The high contribution by phytoplankton to annual primary production (43 - 55 %) in the open water habitat were rather unexpected because high flow conditions in the St. Lawrence River are not conducive to phytoplankton biomass accumulation (Hudon et al. 1996, Hudon 2000, Basu et al. 2000). With the exception of the south water mass, phytoplankton biomass (< 5 mgChla m^{-3}) and production (< 100 mgC m^{-2} d^{-1}) were relatively low compared to other European and North American rivers (e.g. Descy et al. 1988, Cole et al. 1991). The importance of phytoplankton to total primary production on an annual basis was due to its presence over the entire ice-free period and to tributary inputs and water mass dynamics particular to Lake St. Pierre. Specifically, disproportionately large inputs of phytoplankton biomass from tributaries relative to their flow were observed; the presence of the deep main channel further enhanced the impacts of these tributaries on phytoplankton dynamics.

The tributaries entering Lake St. Pierre upstream (north water mass) and within (south water mass) represent large sources of nutrients, suspended matter and phytoplankton biomass to Lake St. Pierre, despite their low contribution to total discharge (< 30 %). In particular phytoplankton biomass in the south waters was roughly 6x higher than in the central waters and annual mean production averaged 400 mgC m^{-2} d^{-1}. Given the relatively large flow of the central water masses in comparison with the tributaries, the former would be expected to cover the majority of the surface area of the lake. However, the presence of a deep shipping channel in the center of the lake leads to the preferential flow of the central water mass in this channel. Waters from the tributaries thus expand their coverage over the lake (~ 50 % of surface area), and in so doing, alter the physical and chemical characteristics occurring over the majority of the lake. This effect was further enhanced under low flow and water level conditions observed in 2001.

Effects of low water level conditions on primary production - Under low flow and water levels in 2001, the coverage by marsh habitat decreased by 50 % and was replaced by a dry meadow type habitat with a higher biomass of robust emergent vegetation and a subsequent drop in algal production within the wetland habitat. Despite the minor contributions of algal production to total wetland primary production, the decline in algae may have had a large impact on secondary production within this habitat as stable isotopes studies have demonstrated that microalgae (attached and phytoplankton) are the dominant food sources in wetlands (i.e. Hart and Lovvorn 2003) and floodplain lakes (i.e. Lewis et al. 2001). In addition, the various classes of wetland (meadow, marsh and mudflat) represent very different types of habitats (dry vs wet) influencing the distribution and diversity of invertebrates, fish and waterfowl. The majority of carbon produced in the open water habitat is exported from the system, whereas carbon production in the wetland zone is likely largely processed within the system. The ecological impacts of shifts in the type and amount of primary production on ecosystem metabolism and on higher trophic levels within the wetland habitat requires further study.

Phytoplankton biomass increased in all water masses between 2000 and 2001. Increases in phytoplankton biomass and production with decreasing flow have been previously observed in other river systems (e.g. Sellers and Bukaveckas 2003), although the opposite trend was previously reported in the St. Lawrence River (Hudon 2000). Annual estimates of phytoplankton production rose by 60 % in the open water habitat between 2000 and 2001. This increase was attributable to the combined effects of a general increase in algal biomass, water temperature and light availability in the water column, and to an increase in the surface area covered by the south water mass. The increase in water temperature (~1° C) in 2001 resulted in higher rates of photosynthesis. Productivity responds strongly to temperature in the St. Lawrence River, exemplified by its relatively high Q_{10} (Q_{10} = 2.45, 95 % CI = 1.8 - 3.4) compared to other systems (Jones 1998, Morin et al. 1999). Shallower water depths in 2001 also resulted in increased bottom light intensities over the majority of the lake (whole lake average of 2 % in 2000 rose to 6% in 2001). In simultaneous measurements of productivity by epiphyton and phytoplankton, we found that photosynthetic parameters (P_{max}^{B} and α^{B})

were consistently higher for phytoplankton than for epiphytes (10x for P_{max} and 5x for α). As a result, phytoplankton are able to use light more efficiently and take advantage of increases in light in the water column under low water levels, whereas epiphyton production changed little in response to decreased water levels .

Whole-system production by macrophyte and epiphyton showed only minor variations in response to changing water levels in 2001, in part because of the small variations in physical conditions in the open water habitat between years. Despite large differences in flow and water levels in the main channel between 2000 and 2001, water depth, current speed and light conditions over most of the surface of the lake did not vary significantly between years. Water depth in the main channel declined by 50-75 cm depending on the season, but because of a loss of wetted surface area and shifts in the distribution of water masses, resulting changes in water depth and light conditions were on average much smaller.

Increases in SAV biomass with decreasing flow have been found in many temperate river systems (see French and Chambers 1997) and direct field-measures demonstrated an increase in SAV biomass in Lake St. Pierre from 67.5 to 80.5 g dry m^{-2} ($p = 0.04$, $n = 41$, paired t-test = -1.77). GIS-modeled estimates for the open water habitat did not indicate significant increases either in mean or total SAV biomass, largely because increases along the north shore (where the majority of field transects were taken) were cancelled out by decreases in SAV biomass in the southern section of the lake. If only the north region of the lake was considered, modeled-derived estimates of SAV biomass increased from a mean of 51.8 g dry m^{-2} to 58.9 g dry m^{-2} between years. Similarly, SAV biomass increased by ~ 20 g dry m^{-2} on the shoals within the central water mass. Such differences emphasize the importance of considering the entire lake area when determining the response of autotrophic communities to changing water levels. Changes in primary production are dependent on local physical changes, which in spatially complex systems such as Lake St. Pierre, were not uniform throughout the lake.

Under low flow conditions in 2001, large masses of filamentous algae were observed, and if included in annual production calculations, filamentous algae would have contributed 8 % to total primary production. Filamentous algae have higher rates

of productivity than attached communities (Chapter 3), and thereby have a competitive advantage under conditions of low water levels because they saturate at a higher irradiance compared to attached forms (Turner et al. 1991). Our estimate here remains, however, preliminary, as these communities were ephemeral in both time and space and poorly sampled by methods adapted to epiphytes (small sampled area) or macrophytes (one sampling date). Nonetheless, other studies have shown that the contribution of filamentous algal mats to primary production can be very high (Robinson et al. 1997, Dalsgaard 2003) and increased under low flow conditions in enriched rivers (Suren et al. 2003). Ecologically, filamentous algal mats increase habitat complexity and provide habitat for benthic invertebrates (Power 1990, Vetter 1994). High amounts of algae can however, stress benthic fauna, through oxygen deficiency (Norkko et al. 2000). Clearly, the ecological role of filamentous algal mats in relation to flow in large rivers should be determined in future studies.

Autotrophic production in large river systems - Results of this study highlight that the amount, type and distribution of primary production in large rivers are determined mainly by physical variables and unique characteristics of individual rivers (flow regime and morphometry). Although autotrophic production was principally governed by physical features as in many river systems, the factors influencing the various producing groups varied and were reflective of the distinct characteristics of Lake St. Pierre. In Lake St. Pierre, submerged macrophytes were strongly dependent on exposure to wind and currents, epiphyton on surface area available for colonization and phytoplankton on tributary inputs. Physical and chemical water conditions within the lake were primarily dependent on the distribution of water masses. As a consequence, the response of this system to decreased water levels was also distinct.

The regulation of flow and the increases in agricultural and urban activities within its drainage basin have led to increases in autotrophic production in Lake St. Pierre. Annual primary production (83 - 99 gC m^{-2} yr^{-1}) remains, however, relatively low compared with other stream and river systems (mean 560 range 3.5 - 5400 gC m^{-2} yr^{-1} - Lamberti and Steinman 1997) or compared to lakes with similar nutrient status

(Wetzel 2001). Physical constraints imposed by strong seasonal cycles in hydrology, temperature and ice-conditions likely maintain the relatively low autotrophic production.

The response of this system to low flow conditions was accentuated by the disturbances it has already experienced. The dredging of the main channel altered the hydrology and distribution of water masses in the river, which increased the influence of nutrient-rich tributary inputs on the distribution and magnitude of primary production. Under low water conditions, the surface area covered by nutrient-rich tributaries further increased and resulted in further shifts towards increased phytoplankton production and spatial changes in production by SAV and associated epiphytes. The central water mass contributed the most to production in 2000, with a dominance by macrophytes and epiphyton. In 2001, under low water levels, phytoplankton in the south water mass became the dominant producer in the lake. The response of this large fluvial lake to decreased flow was thus the result of complex interactions between physical changes related directly to flow (i.e. water depth) which were modified by human activities (presence of main channel, tributary inputs).

The spatial complexity in physical conditions and resulting distribution of autotrophic production were high. As the water masses of Lake St. Pierre present major differences in physical and chemical characteristics within the lake, autotrophic primary production was largely dependent on their distribution. One of the limitations of the GIS-modeling approach in this study was the use of static hydrological conditions within given seasons for the delimitation of the various water masses in Lake St. Pierre. Flow and water level conditions vary daily, and because the distribution of the various water masses is the cumulative result of flow from the Great Lakes and the tributaries, the distribution of the various water masses also varies spatially and temporally. Major distinctions between water masses were visible, but gradients in mixing among them occur and are dynamic in both space and time. Our identification of the mixed water mass was an attempt to include some of this variability, although limited sampling along south shore prevented us from considering gradients within this area. Nonetheless, the GIS-based approach used in this study provided spatially-explicit estimates which reflected the major differences in physical conditions throughout the lake and this type

of approach was fundamental to the understanding of the relative importance of primary producers within Lake St. Pierre.

This study represents one of the first estimates of whole-system production of all primary producers in a large river system. Spatially-explicit whole-system carbon budgets show that algal production dominated carbon budgets (60 %) but emergent and submerged macrophytes were also important contributors to autotrophic production at the scale of the lake. GIS-based models revealed the spatial complexities in the type and magnitude of primary production within the open water habitat of the lake. Temporal changes in production also varied between primary producer communities and between years with different flow and water level conditions, likely influencing ecosystem metabolism and the dynamics of higher trophic levels. As climate change further alters flow regimes in large rivers systems, future regulation of flow should consider the important spatial and temporal variations in production across all riverine habitats.

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CONCLUSIONS GÉNÉRALES

Cette thèse représente la première estimation de la production primaire totale du Lac Saint-Pierre, par type de producteurs et l'une des premières estimations quantitatives de l'importance relative des producteurs autotrophes dans une grande rivière qui tient compte de l'hétérogénéité spatiale de ce type de système. L'approche développée au cours de cette thèse, en combinant des méthodes classiques (mesures de production primaire) avec des outils technologiques récents, (SIG et télédétection) représente une contribution originale à l'estimation de la production totale à grande échelle. Les résultats sur la photosynthèse des algues épiphytiques et algues filamenteuses apportent aussi une source d'informations nouvelles car la productivité de ces communautés est actuellement peu connue. Finalement, les conséquences des changements du régime de débits et des niveaux d'eau du fleuve Saint-Laurent sur la production primaire totale sur le Lac Saint-Pierre ont été mises en évidence.

Les résultats des deux premiers chapitres de cette thèse sont basés sur l'utilisation des SIGs et de la télédétection, en combinaison avec des données de terrain et des modèles empiriques, comme une approche pour estimer la production primaire à grande échelle. Malgré que les macrophytes ont déjà été modélisées par ce type d'approche (e.g. Lehmann 1998), les diverses méthodes qui produisent des cartes de distribution de macrophytes à grande échelle n'ont jamais été comparées entre elles. Bien que la télédétection et l'écho-sondage soient utiles pour caractériser la distribution des groupements de plantes vasculaires de la plaine inondable (Létourneau et al. 1996) et dans les eaux libres (Fortin et al. 1993) respectivement, ces méthodes ne caractérisent pas la zone de transition entre les milieux terrestres et aquatiques. Seuls les modèles empiriques ont pu apporter une perspective sur l'ensemble des habitats de plantes en rivière et une estimation quantitative de la biomasse de macrophytes (Chapitre 1) qui, par la suite, peut servir à estimer quantitativement la lumière et la productivité algale à l'échelle du lac. Ceci représente un élément important conduisant à une meilleure compréhension de la dynamique des communautés de plantes face aux changements des niveaux d'eau.

La production primaire par le phytoplancton est bien décrite dans la littérature et de nombreux modèles empiriques existent pour modéliser la productivité de cette communauté (Behrenfeld & Falkowski 1997). Les estimations de production totale à l'échelle du lac ou du système sont souvent basées sur la profondeur moyenne du système. Une grande partie de hétérogénéité spatiale dans la production primaire du Lac Saint-Pierre est due aux variations de profondeur de l'eau (Chapitre 2), tel que démontré dans d'autres systèmes aquatiques (Fee 1980, Millard et al. 1999). En tenant compte des différences de profondeur optique dans l'estimation de la production primaire, un modèle empirique général décrit dans le second chapitre permet une application spatiale des modèles empiriques dans des milieux optiquement complexes tels que le fleuve Saint-Laurent.

La production primaire des algues épiphytiques reste peu connue en comparaison de celle du phytoplancton (Wetzel 2001). L'étude sur la production primaire des algues épiphytiques ainsi que des algues filamenteuses du fleuve Saint-Laurent a démontré que les paramètres photosynthétiques des épiphytes sont fortement reliés à la biomasse algale (Chapitre 3). Cependant, la lumière *in situ* et les variations de lumière en fonction de la profondeur influencent aussi la production primaire de ces communautés attachées. Les résultats du troisième chapitre montrent que les variations verticales dans la disponibilité du substrat (macrophytes), de la biomasse des épiphytes, de la lumière et de la réponse photosynthétique jouent un rôle important dans l'estimation de la production primaire par unité de surface de lac et par conséquent, à grande échelle.

Les mesures de production faites durant deux années montrent que les masses d'algues filamenteuses qui flottent à la surface utilisent la lumière de manière plus efficace que les algues attachées (Chapitre 3). Ceci confère à ces organismes un avantage face aux changements des niveaux d'eaux car, avec une augmentation de la lumière disponible dans la colonne d'eau, leur productivité augmente comparée aux algues attachées dont la productivité sature à une irradiance plus faible. L'augmentation de la biomasse et de la production observée et modélisée pour ces algues en conditions de bas niveaux peut avoir un impact important sur le transfert du carbone, le recyclage des nutriments, et la respiration. Pour les algues filamenteuses, les estimés de production à l'échelle du lac restent approximatifs, dus à la méthode d'échantillonnage. Cependant, ils

indiquent que de plus amples études sont nécessaires pour déterminer la dynamique des algues filamenteuses face à des changements de débits.

La majorité des théories sur le fonctionnement des grandes rivières mettent l'emphase sur l'importance du carbone allochtone (e.g. Vannote et al. 1980). Cependant, quelques modèles conceptuels estiment que la production autochtone de carbone peut être importante dans des grandes rivières, lorsque les facteurs physiques tels que la profondeur de l'eau, la lumière et le débit sont favorables aux développement des plantes (Thorp & Delong 1994, Reynolds & Descy 1996, Wetzel & Ward 1996). Les résultats de l'analyse de la contribution des producteurs à grande échelle, présentés dans le quatrième chapitre, montrent que les contributions par les macrophytes et les épiphytes sont aussi importantes que celle du phytoplancton dans le Lac Saint-Pierre. Considérant la zone peu profonde du Lac Saint-Pierre, qui s'étend sur des kilomètres, l'importance des macrophytes et des épiphytes n'est pas suprenante. Cependant, les contraintes physiques limitent la productivité: les fortes expositions au vent et aux courants sont responsables d'une production primaire totale relativement faible pour les conditions de lumière et de nutriments présentes dans le milieu (Wetzel 2001). De plus, les macrophytes et les épiphytes montrent de fortes variations saisonnières qui limitent leur contribution relative à la production totale annuelle. Le phytoplancton contribue à plus de 40% de la production totale du système, en raison de sa présence durant toute la saison sans glace et aux apports des tributaires. Les tributaires de la rive nord et sud du lac couvrent plus de la moitié de la surface totale du lac et les eaux brunes apportent de fortes charges en biomasse de phytoplancton et en matière en suspension influençant ainsi l'ensemble de la dynamique du carbone dans ce système.

Les modèles géographiques prédictifs apportent une vision nouvelle à la production primaire et permet d'incorporer la complexité spatiale des systèmes. Par contre, l'approche utilisée dans ce travail, comme toute modélisation, représente une simplification de la réalité et est associée à une erreur. Les limitations des suppositions et de la modélisation ont été discutées pour chaque producteur dans chacun des chapitres. La propagation des erreurs dues aux modèles a aussi été prise en considération par des simulations Monte Carlo, présentées dans le dernier chapitre. La plus grande erreur a été observée pour les estimés de production des épiphytes. Pour cette communauté, une

meilleure estimation de sa contribution devrait inclure une intégration verticale à l'intérieur du SIG, comme les résultats du troisième chapitre le démontrent. L'erreur calculée apporte une information supplémentaire sur l'estimation à grande échelle bien que son mode de calcul reste encore à développer dans le cas de la modélisation en SIG car les erreurs spatiales ne sont pas encore prises en compte par cette méthode.

La reconnaissance des apports en nutriments et en biomasse algale des tributaires du Lac Saint-Pierre est un résultat important qui souligne l'effet néfaste de ces rivières sur le fonctionnement du fleuve, surtout dans le cas d'une diminution du débit. La présence de la voie maritime et son dragage continu ont un grande influence sur l'hydrologie du système et la distribution des masses d'eau dans le Lac Saint-Pierre, qui en conséquence influencent la biologie du système. Auparavant, les eaux provenant des Grands Lacs, en raison de leurs forts débits comparés à ceux des tributaires, occupaient probablement une plus grande superficie du Lac St. Pierre. Aujourd'hui, les eaux des rivières Yamaska, Richelieu et Saint-François sont responsables de plus de 50% de la production globale du Lac Saint-Pierre, même si ces cours d'eau ne représentent que moins du tiers du débit total du lac. Avec un abaissement des niveaux et la présence du chenal de navigation, l'impact de ces tributaires sur les contributions relatives des producteurs primaires est encore plus grand.

Les résultats de cette étude permettent une meilleure compréhension du transfert de carbone et les méthodes décrites et les résultats pourront servir à d'autres recherches sur le fonctionnement écologique des grandes rivières. Les fluctuations importantes du niveau du Lac Saint-Pierre lors des dernières années ont souligné le fait que ces changements pouvaient avoir des conséquences sociales, économiques et écologiques. Les effets d'une augmentation de la biomasse et de la production du phytoplancton et les apports importants de la production par les macrophytes et les épiphytes sur la production secondaire dans le Lac Saint-Pierre restent à déterminer. Bien que le fleuve ait subi des pertubations majeures dans son histoire (incluant le dragage d'une voie de navigation et des apports importants en nutriments), la nature est prospère au Lac Saint-Pierre. En raison de ses caractéristiques physiques, le fleuve Saint-Laurent était probablement oligotrophe dans le passé, mais suite aux augmentations en apports de nutriments et au régularisation du débit, la production primaire de tous les producteurs a augmenté.

Aujourd'hui, la diminution du débit favorise la productivité du phytoplancton et des algues filamenteuses. Bien que l'estimation de production primaire dans cette thèse ne représente qu'une première étape dans la compréhension du fonctionnement des grandes rivières, les résultats mettent en évidence les effets d'une diminution des niveaux d'eau. Il est à espérer que ce travail pourra servir à une meilleure gestion des niveaux d'eau du fleuve.

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ANNEXE I. *Relations entre la photosynthèse et la lumière(P-I) pour les communautés épiphytiques du lac Saint-Pierre en 2000 et 2001.*

Les moyennes (± S.E.) sont présentées (n = 3 ou 2). Les valeurs originales en oxygène ont été converties en unité de carbone en supposant un coefficient de photosynthèse de 1.25. Les abréviations sont les suivantes: GPP correspond à la production primaire brute (ou 'gross primary production'); epi-sub correspond aux mesures faites sur les feuilles des plantes submergées en plastique; fila correspond aux mesures faites sur des tapis d'algues filamenteuses; epi-emer correspond aux mesures faites sur les tiges en plastiques installées parmi les plantes émergentes. Les données sont ajustées au modèle de Jassby et Platt 1976, les valeurs non utilisées étant indiquées par des cercles vides (irradiance >> 1000 µmol m^{-2} s^{-1}). Les données des graphiques sans courbes n'ont pas été modélisées et sont exclues des analyses de la thèse. Sur chaque graphique, la date, le type de communauté, la profondeur d'eau d'où proviennent les échantillons sont indiqués (en mètres de la surface) ainsi que les valeurs de Pbm (taux maximal de la photosynthèse brute en mgC $mgChla^{-1}$ h^{-1}) et de α (pente initiale de la courbe P-I en mgC (mgChl a^{-1}) h^{-1}(µmol m^{-2} s^{-1}) $^{-1}$.

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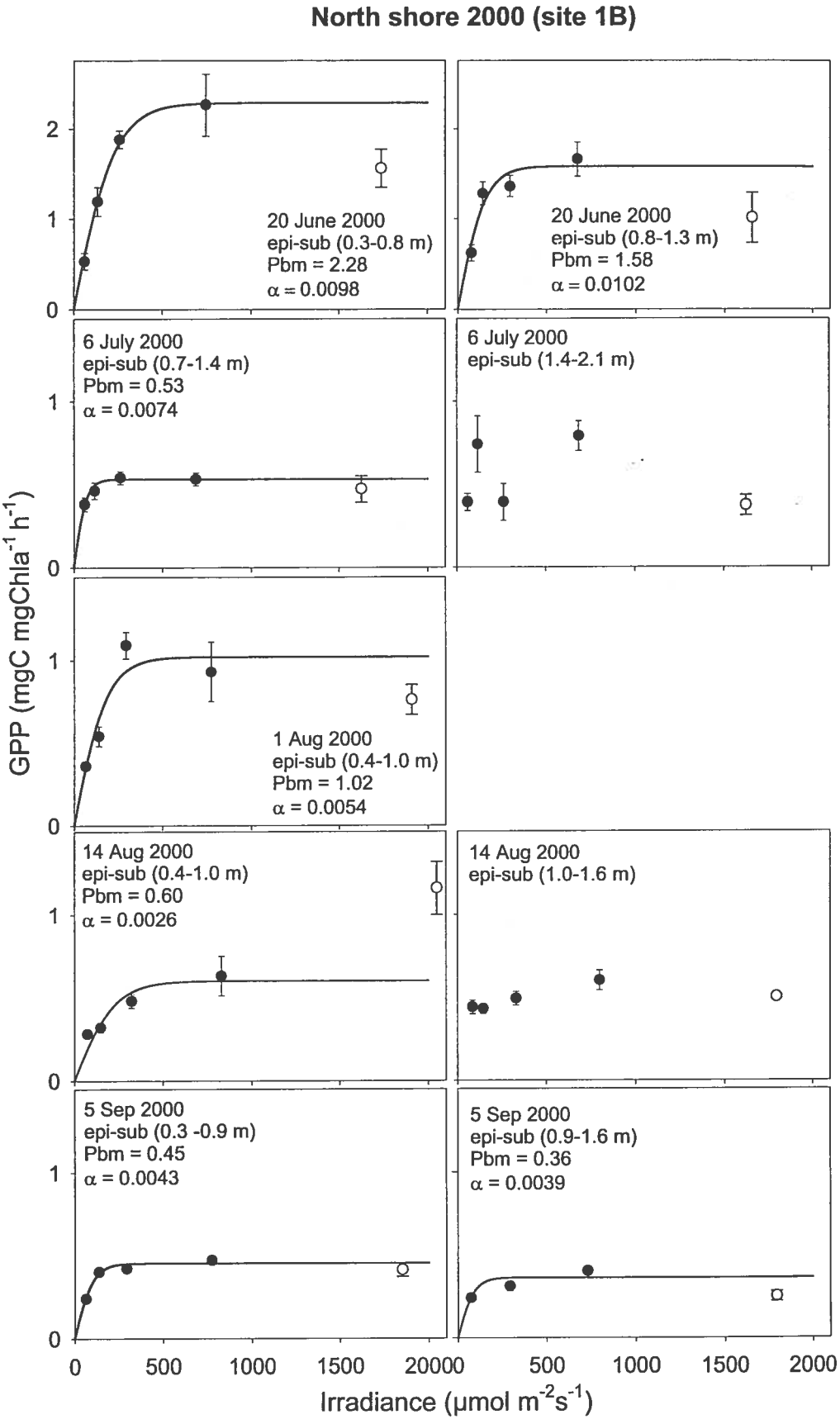
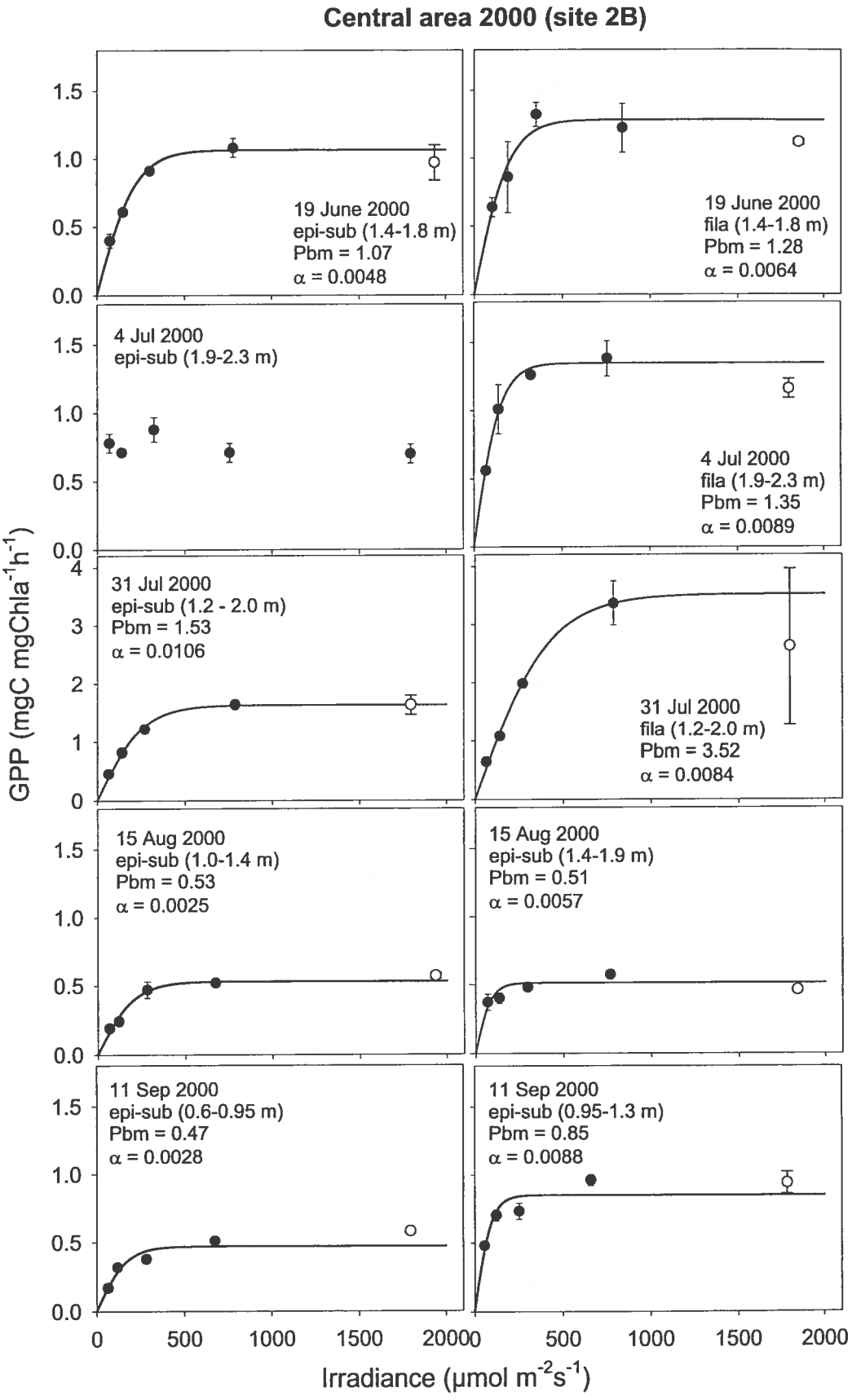
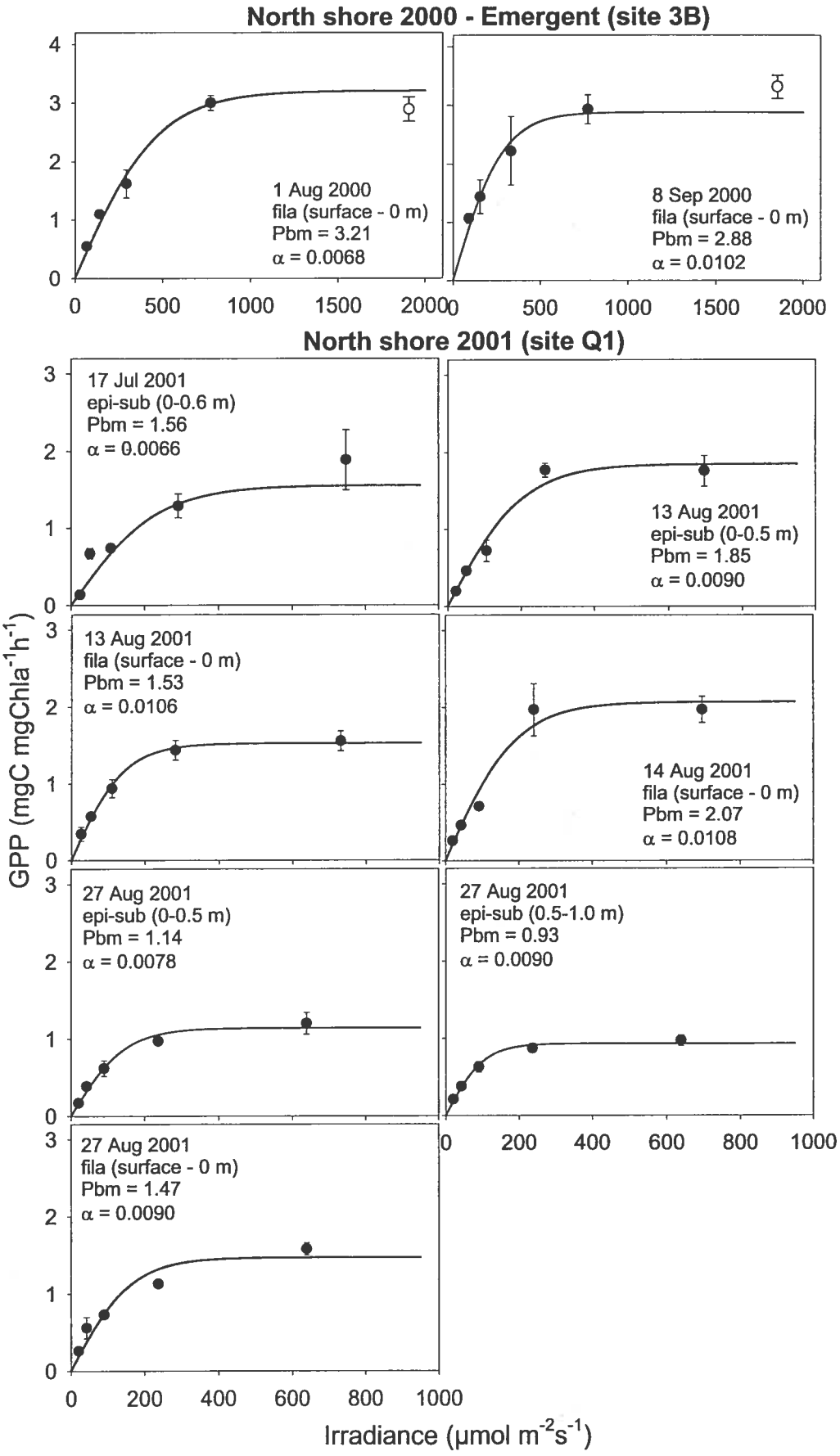
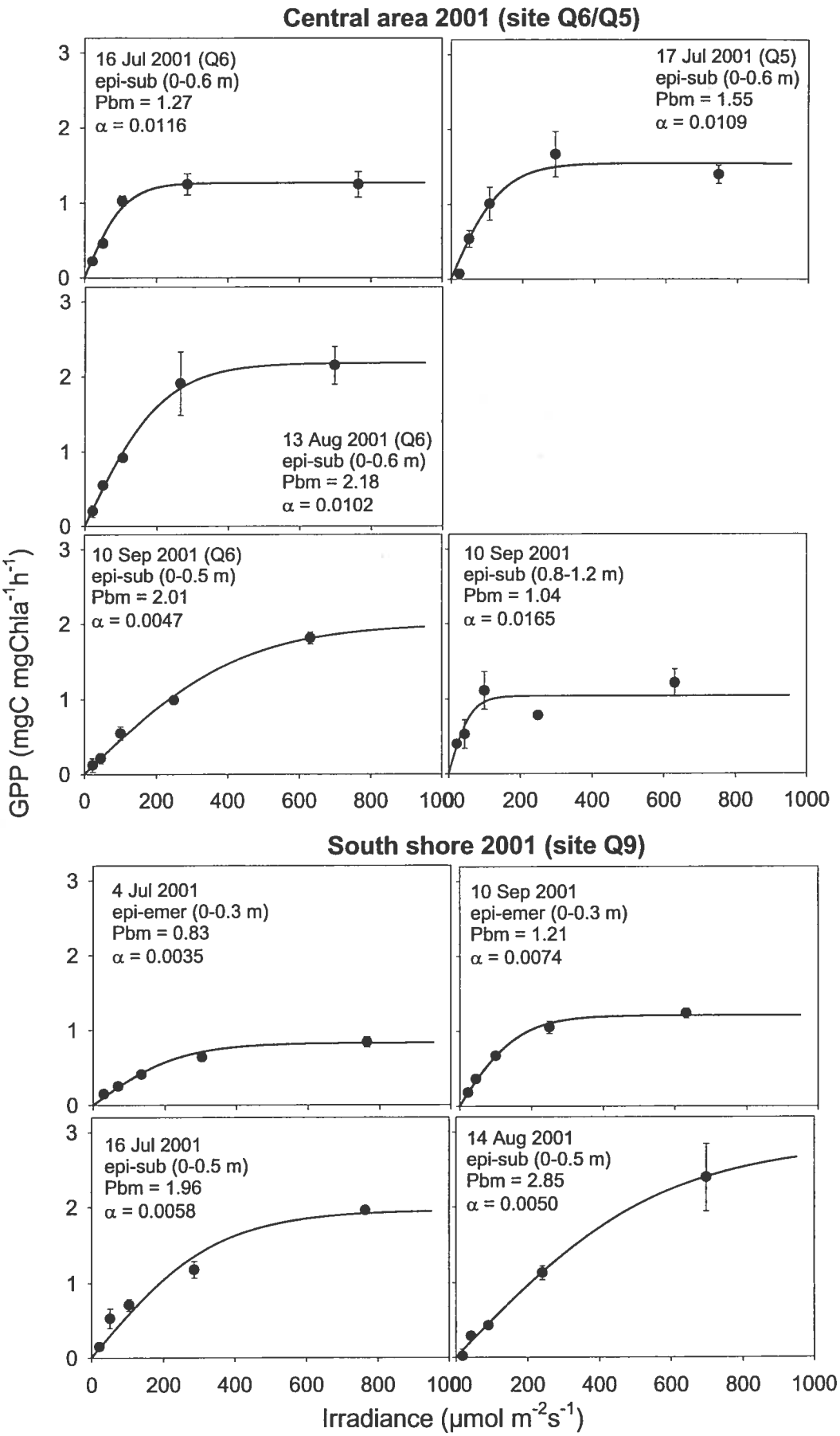

North shore 2000 (site 1B)
20 June 2000
epi-sub (0.3-0.8 m)
Pbm = 2.28
α = 0.0098
20 June 2000
epi-sub (0.8-1.3 m)
Pbm = 1.58
α = 0.0102
6 July 2000
epi-sub (0.7-1.4 m)
Pbm = 0.53
α = 0.0074
6 July 2000
epi-sub (1.4-2.1 m)
1 Aug 2000
epi-sub (0.4-1.0 m)
Pbm = 1.02
α = 0.0054
14 Aug 2000
epi-sub (0.4-1.0 m)
Pbm = 0.60
α = 0.0026
14 Aug 2000
epi-sub (1.0-1.6 m)
5 Sep 2000
epi-sub (0.3 -0.9 m)
Pbm = 0.45
α = 0.0043
5 Sep 2000
epi-sub (0.9-1.6 m)
Pbm = 0.36
α = 0.0039
GPP (mgC mgChla-1 h-1)
Irradiance (µmol m-2s-1)
0
1
2
500
1000
1500
20000
2000


Central area 2000 (site 2B)
19 June 2000
epi-sub (1.4-1.8 m)
Pbm = 1.07
α = 0.0048
19 June 2000
fila (1.4-1.8 m)
Pbm = 1.28
α = 0.0064
4 Jul 2000
epi-sub (1.9-2.3 m)
4 Jul 2000
fila (1.9-2.3 m)
Pbm = 1.35
α = 0.0089
31 Jul 2000
epi-sub (1.2 - 2.0 m)
Pbm = 1.53
α = 0.0106
31 Jul 2000
fila (1.2-2.0 m)
Pbm = 3.52
α = 0.0084
15 Aug 2000
epi-sub (1.0-1.4 m)
Pbm = 0.53
α = 0.0025
15 Aug 2000
epi-sub (1.4-1.9 m)
Pbm = 0.51
α = 0.0057
11 Sep 2000
epi-sub (0.6-0.95 m)
Pbm = 0.47
α = 0.0028
11 Sep 2000
epi-sub (0.95-1.3 m)
Pbm = 0.85
α = 0.0088
GPP (mgC mgChla-1h-1)
Irradiance (µmol m-2s-1)
0
500
1000
1500
20000
500
1000
1500
2000

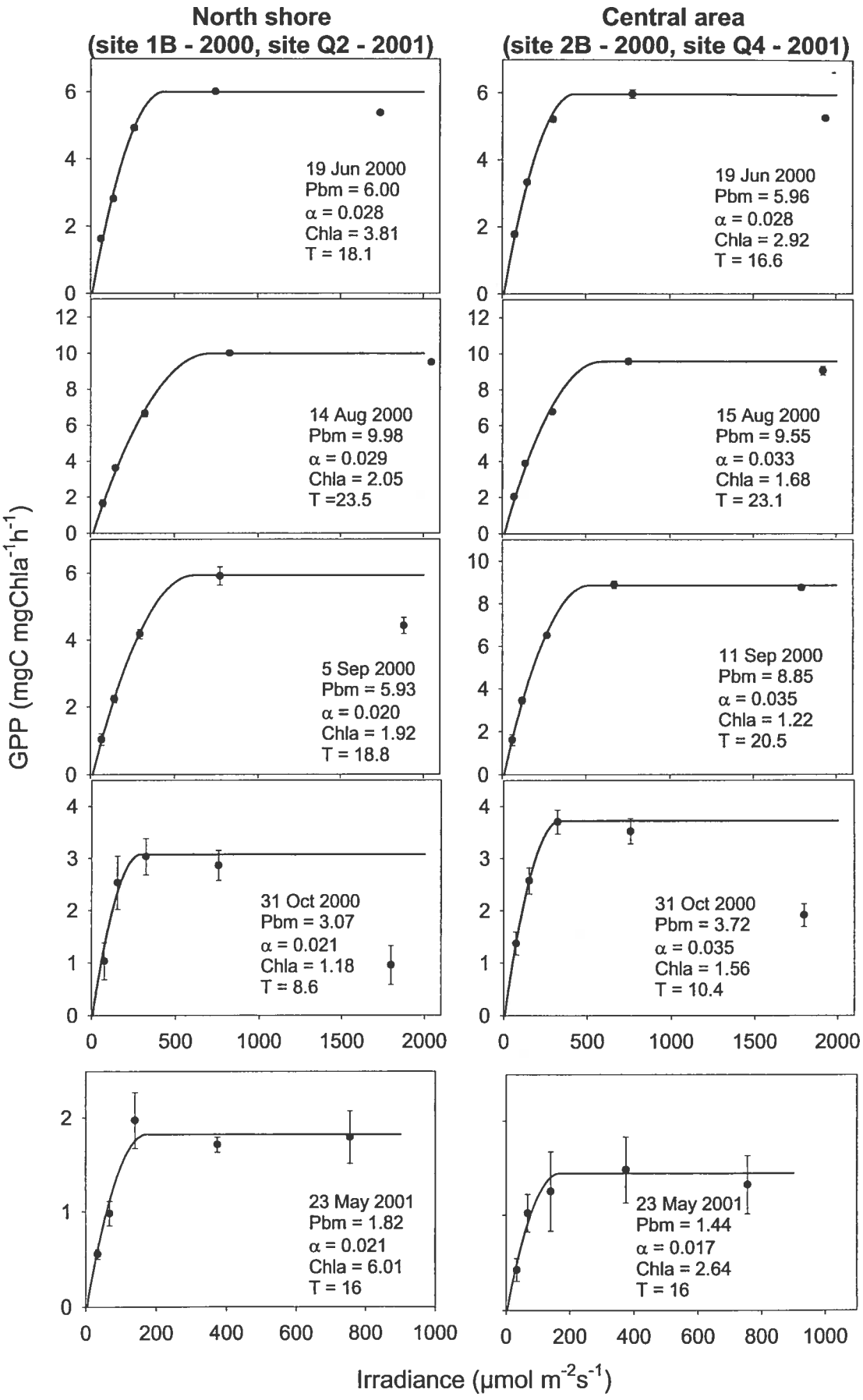

North shore 2000 - Emergent (site 3B)
1 Aug 2000
fila (surface - 0 m)
Pbm = 3.21
α = 0.0068
8 Sep 2000
fila (surface - 0 m)
Pbm = 2.88
α = 0.0102
North shore 2001 (site Q1)
17 Jul 2001
epi-sub (0-0.6 m)
Pbm = 1.56
α = 0.0066
13 Aug 2001
epi-sub (0-0.5 m)
Pbm = 1.85
α = 0.0090
13 Aug 2001
fila (surface - 0 m)
Pbm = 1.53
α = 0.0106
14 Aug 2001
fila (surface - 0 m)
Pbm = 2.07
α = 0.0108
27 Aug 2001
epi-sub (0-0.5 m)
Pbm = 1.14
α = 0.0078
27 Aug 2001
epi-sub (0.5-1.0 m)
Pbm = 0.93
α = 0.0090
27 Aug 2001
fila (surface - 0 m)
Pbm = 1.47
α = 0.0090
GPP (mgC mgChla-1h-1)
Irradiance (µmol m-2s-1)

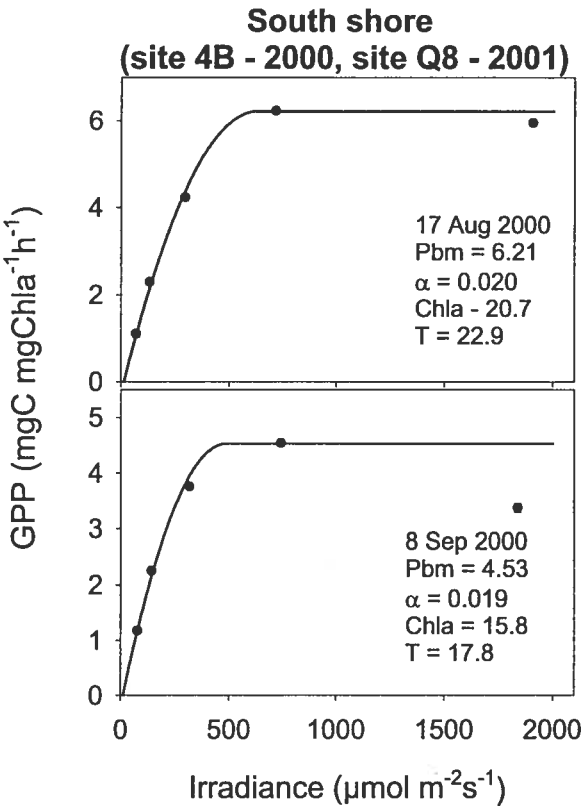

Central area 2001 (site Q6/Q5)
16 Jul 2001 (Q6)
epi-sub (0-0.6 m)
Pbm = 1.27
α = 0.0116
17 Jul 2001 (Q5)
epi-sub (0-0.6 m)
Pbm = 1.55
α = 0.0109
13 Aug 2001 (Q6)
epi-sub (0-0.6 m)
Pbm = 2.18
α = 0.0102
10 Sep 2001 (Q6)
epi-sub (0-0.5 m)
Pbm = 2.01
α = 0.0047
10 Sep 2001
epi-sub (0.8-1.2 m)
Pbm = 1.04
α = 0.0165
GPP (mgC mgChla-1h-1)
South shore 2001 (site Q9)
4 Jul 2001
epi-emer (0-0.3 m)
Pbm = 0.83
α = 0.0035
10 Sep 2001
epi-emer (0-0.3 m)
Pbm = 1.21
α = 0.0074
16 Jul 2001
epi-sub (0-0.5 m)
Pbm = 1.96
α = 0.0058
14 Aug 2001
epi-sub (0-0.5 m)
Pbm = 2.85
α = 0.0050
Irradiance (µmol m-2s-1)

ANNEXE II. *Relations entre la photosynthèse et la lumière (P-I) pour le phytoplancton du lac Saint-Pierre en 2000 et 2001.*

Les moyennes (± S.E.) sont présentées (n=3). Les valeurs originales en oxygène ont été converties en unité de carbone en supposant un coefficient de photosynthèse de 1.25. GPP correspond à la production primaire brute (gross primary production) (mgC $mgChla^{-1}$ h^{-1}). Les données sont ajustées au modèle de Fee (1990), et les valeurs non utilisées sont indiquées par des cercles vides (irradiance >> 1000 µmol m^{-2} s^{-1}). Les données des graphiques sans courbe n'ont pas été modélisées et ont été exclues des analyses. Sur chaque graphique, la date, les valeurs Pbm (le taux maximal de la photosynthèse brute en mgC $mgChla^{-1}$ h^{-1}) et α (pente initiale de la courbe P-I en mgC (mgChl a^{-1}) h^{-1}(µmol m^{-2} s^{-1}) $^{-1}$, la concentration en Chla (mg m^{-3}) et la température de l'eau (°C) sont indiqués.

Fee, E.J. 1990. Computer programs for calculating in situ phytoplankton photosynthesis. Can. Tech. Rep. Fish. Aquat. Sci. No. 1740.


North shore
(site 1B - 2000, site Q2 - 2001)
Central area
(site 2B - 2000, site Q4 - 2001)
19 Jun 2000
Pbm = 6.00
α = 0.028
Chla = 3.81
T = 18.1
19 Jun 2000
Pbm = 5.96
α = 0.028
Chla = 2.92
T = 16.6
14 Aug 2000
Pbm = 9.98
α = 0.029
Chla = 2.05
T =23.5
15 Aug 2000
Pbm = 9.55
α = 0.033
Chla = 1.68
T = 23.1
5 Sep 2000
Pbm = 5.93
α = 0.020
Chla = 1.92
T = 18.8
11 Sep 2000
Pbm = 8.85
α = 0.035
Chla = 1.22
T = 20.5
31 Oct 2000
Pbm = 3.07
α = 0.021
Chla = 1.18
T = 8.6
31 Oct 2000
Pbm = 3.72
α = 0.035
Chla = 1.56
T = 10.4
23 May 2001
Pbm = 1.82
α = 0.021
Chla = 6.01
T = 16
23 May 2001
Pbm = 1.44
α = 0.017
Chla = 2.64
T = 16
GPP (mgC mgChla-1h-1)
Irradiance (µmol m-2s-1)


South shore
(site 4B - 2000, site Q8 - 2001)
GPP (mgC mgChla-1h-1)
17 Aug 2000
Pbm = 6.21
α = 0.020
Chla - 20.7
T = 22.9
8 Sep 2000
Pbm = 4.53
α = 0.019
Chla = 15.8
T = 17.8
0
2
4
6
0
1
2
3
4
5
0
500
1000
1500
2000
Irradiance (µmol m-2s-1)

ANNEXE III. *Informations supplémentaires sur les macrophytes submergées et émergentes qui ont servi au calcul de la production épiphytique.*

A. Distribution verticale de la biomasse des macrophytes submergées.

En 2000 et 2001, des plantes entières ont été récoltées et divisées en trois sections égales afin de déterminer la distribution verticale de la biomasse des épiphytes et des macrophytes. Les biomasses d'épiphytes étaient trop variables pour faire ressortir les tendances alors que la distribution verticale de la biomasse des macrophytes submergées ont démontré des tendances par espèces. Nous avons ajouté les données de Christiane Hudon pour augmenter le nombre d'observations. Suite à une analyse de groupement, quatre groupes de plantes avec une distribution verticales de biomasses semblables ont été identifiés et ces données ont servi au calcul de la production des épiphytes par unité de surface.

		% de la biomasse total par section moyenne ± écartype (% utiliser)			
groupe	Espéces	haut	centre	bas	n
1	*Vallisneria americana*	26 ± 4 (25%)	30 ± 7 (30%)	44 ± 8 (45%)	7
2	*Ceratophyllum demersum*	40 (40%)	54 (55%)	6 (5%)	1
3	*Myriophyllum* sp., *Potamogeton richardsonii*, *P. pectinatus*, *Elodea canadensis*	56 ± 16 (55%)	25 ± 8 (25%)	19 ± 10 (20%)	5
4	*Heteranthera dubia*, *Nitella* sp.[a]	74 ± 3 (75%)		26 ± 3 (25%)	2

[a] Aucun échantillon de *Nitella* n'étant mesuré, ce genre a été assigné au groupe 4, basé sur sa forme de croissance.

B. Composition de la biomasse des quadrats dans les zones émergentes.

Chaque espèce de macrophyte émergente, en raison de sa forme et architecture, présente une surface de substrat différente disponible pour la croissance épiphytique. La composition spécifique dans les quadrats de biomasse était déterminée à partir des mesures de terrain en 2000 et 2001 (Hudon et al. 2004) pour les catégories 'mixte marsh'

et 'scattered marsh' . Ces données ont par la suite servis au calcul de substrat disponible pour les épiphytes.

Type	% cumulé de la biomasse moyenne Calculé	Utilisé
Espèces submergées	0.2	0
S. lacustris - ou forme linéaire	58	60
Typha	12	15
Sagittaire	18	20
Phalaris - graminées	6	5
Bolbochoenus - S. fluviatilis	0.9	0

C. Relation entre la fraction cumulée de la biomasse sèche totale et la longueur cumulée de la plante (cm).

Seulement une partie des plantes émergentes est imergée et donc disponible comme substrat pour les épiphytes. J'ai utilisé des relations développées par C. Hudon (données non publiées) pour calculer la fraction de la biomasse des espèces émergentes dans l'eau.

Type	% biomasse = ax^b ou x = longueur cumulée de la plante (cm) ou la profondeur de l'eau a	b
S. lacustris - ou forme linéaire	0.7016	1.0437
Typha	1.3173	0.8784
Sagittaire	2.9146	0.8166
Phalaris - graminées	1.1676	0.9773

Hudon, C., Gagnon, P., Amyot, J.-P., Letourneau, G., Jean, M., Plante, C., Rioux, D. and Deschenes, M. 2004. Historical changes in herbaceous wetland distribution and biomass: effects of hydrology on faunal habitats in Lake St. Pierre (St. Lawrence River, Quebec, Canada). St. Lawrence Centre, Environment Canada. Report.

ANNEXE IV. *Données physiques, chimiques et biologiques mesurés au Lac St. Pierre en 2000 et 2001.*

En tête	Description (unité)
date	la date échantillonnée
site	no. de site
X	longitude (m) mesurée avec un GPS (UTM nad83 zone 18)
Y	latitude (m) mesurée avec un GPS (UTM nad83 zone 18)
water	masse d'eau
MMB	Biomasse maximale de macrophytes (g poids sec m^{-2})
Zt	Profondeur totale (m)
Temp	Température de l'eau (°C) mesurée à 20 cm de la surface avec un Hydrolab
Cond	Conductivité (µS cm^{-1}) mesurée à 20 cm de la surface avec un Hydrolab
pH	pH mesuré à 20 cm de la surface avec un Hydrolab
Courant	Courant mesuré à 20cm sous la surface de l'eau (m s^{-1})
MES	Matières en suspension (mg L-1)
A440	Absorbance de l'eau filtrée (Whatman GF/C) à 440 nm
Ktotal	Coefficient d'atténuation lumineux total (m^{-1}) - inclus l'effet des plantes (moyenne et écart type (s.d.) de n profiles)
type	type de profile: 1- eau seulement, 2- mixte (eau et plantes - moyenne pondérée pour Ktotal), 3 - plantes dominent
Kwater	Coefficient d'atténuation lumineuse de l'eau seule (m^{-1})
Kplant et zplant	Coefficient d'atténuation lumineuse des plantes (m^{-1}) et profondeur correspondante (m de la surface)
Phyto ou Chla	Concentration en Chla (mg m^{-3})
Macrophytes	Présence (1) ou absence (0) de plantes submergées (SUBM) ou émergentes (EMER)
Epiphytes - zsam	Profondeur à laquelle les échantillons de biomasses d'épiphytes ont été récoltés (m de la surface)
plant	Espèces de plantes: VALA - *Vallisneria americana*, POTR - *Potamogeton richardsonii*, POTP - *Potamogeton pectinatus*, ELOC - *Elodea canadensis*, MYRS - *Myriophyllum sp.*, HETD - *Heteranthera dubia*, CERD - *Ceratophyllum demersum*, NIT - *Nitella* sp., SCIL - *Scirpus lacustris*, TYPA - *Typha augustifolia*, SPAE - *Sparganium eurycarpum*
Biomasse épiphytique	moyenne (moy), écart type (sd) et nombre de réplicats (N) de la biomasse épiphytique (µg Chla g poids sec de plantes $^{-1}$). Les valeurs représentent la biomasse d'algues détachées par brassage. Pour les convertir en biomasse totale, les pourcentages suivants ont été déterminés: la partie fortement attachée à la plante était en moyenne 35 % de la biomasse totale sur les espèces de plantes submergées en 2000, 25 % de la biomasse totale sur les espèces de plantes submergées en 2001 et 15 % de la biomasse totale sur les espèces de plantes émergentes en 2001.

date	site	X	Y	water	MMB	Zt	Temp	Cond	pH	Courant	MES	A440
04-mai-00	14	659265	5114433	3	0			261				
04-mai-00	23	657419	5115853	4	3			171				
04-mai-00	24	658352	5114760	4	3			246				
04-mai-00	25	659396	5113510	4	3			255				
04-mai-00	26	660141	5112263	4	3							
04-mai-00	27	660402	5111652	4	3			242				
04-mai-00	28	660463	5111388	4	3			154				
11-mai-00	201	657753	5116097	1	108	3,0	10,9	191				
11-mai-00	202			3	41	3,0	10,4	267				
22-mai-00	1	659097	5117810	1	108	2,4	14,0	145	7,3	0,22		
22-mai-00	2	661847	5118814	2	4	4,3	13,5	185	7,5	0,37		
22-mai-00	3	662323	5120608	1	91	3,7	14,2	146	7,4	0,30		
22-mai-00	4	664149	5120134	2	2	4,6	13,3	192	7,6	0,35		
22-mai-00	5	665369	5122661	1	60	3,7	14,1	144	7,4	0,26		
22-mai-00	6	668803	5122565	2	11	4,9	13,8	187	7,5	0,30		
22-mai-00	7	670659	5124624	1	18	4,6	14,0	147	7,4	0,30		
22-mai-00	8	673170	5124598	2	10	5,5	14,2	186	7,5	0,42		
22-mai-00	9	675718	5127074	1	16	3,7	14,4	148	7,4	0,27		
22-mai-00	10	677552	5126760	2	0		14,4	166	7,5	0,35		
22-mai-00	11	678007	5126172	2	0	14,0	14,3	181	7,5	0,50		
22-mai-00	12	673142	5123325	3	0	14,3	13,0	232	7,7			
22-mai-00	13	668448	5119904	3	0	13,7	12,7	234	7,7			
22-mai-00	14	659068	5114405	3	0	14,9	12,7	231	7,7	0,60		
22-mai-00	15	660158	5113761	3	41	2,7	12,6	244	7,7	0,25		
22-mai-00	16	660538	5112372	3	88	2,4	12,6	235	7,0	0,27		
22-mai-00	17	660531	5111483	4	3	2,4	14,1	215	7,5	0,44		
22-mai-00	18	660578	5111357	4	0	1,5	14,4	191	7,5	0,33		
23-mai-00	1	659026	5117752	1	108	2,4	14,3	146	7,6	0,14		
23-mai-00	2	661794	5118895	2	4	4,3	13,8	183	7,7	0,29		
23-mai-00	3	662445	5120781	1	91	3,4	14,2	147	7,6	0,25		
23-mai-00	4	664056	5120565	2	2	4,3	13,8	183	7,7	0,27		
23-mai-00	15	660120	5113846	3	41	2,9	12,8	243	7,9	0,22		
23-mai-00	16	660785	5112291	3	88	2,4	12,6	228	7,9	0,22		
23-mai-00	20	660860	5116065	3	0	15,2	12,9	228	7,8	0,66		
23-mai-00	21	661585	5114851	3	41	3,7	12,6	242	7,9	0,43		
23-mai-00	22	662016	5111612	4	3	2,4	14,5	234	7,6	0,25		
23-mai-00	202	661160	5113960	3	41	2,7	12,6	239	7,9	0,34		
05-juin-00	202	661034	5113912	3	41	2,2	14,8	257	8,1	0,20		
06-juin-00	1	659043	5117794	1	108	1,8	15,9	190	7,8	0,09		
06-juin-00	2	661786	5118563	2	4	3,7	15,3	227	7,9	0,28		
06-juin-00	3	662493	5120665	1	91	2,7	15,9	191	7,8	0,17		
06-juin-00	4	664420	5120111	2	2	3,7	15,3	223	7,9	0,26		
06-juin-00	5	665459	5122643	1	60	3,0	15,7	193	7,8	0,23		
06-juin-00	6	668721	5122657	2	11	4,0	15,6	223	7,9	0,29		
06-juin-00	7	670702	5124721	1	18	3,7	15,8	199	7,8	0,25		
06-juin-00	8	673278	5124826	2	10	4,6	15,9	229	7,9	0,20		
06-juin-00	9	675829	5127167	1	16	3,0	16,2	196	7,8	0,20		
06-juin-00	11	677933	5126129	2	0	13,7	16,0	233	8,0	0,20		
06-juin-00	13	668511	5119985	3	0	13,4	15,1	254	8,1			
06-juin-00	14	659086	5114426	3	0	14,9	15,0	258	8,0			
06-juin-00	15	660462	5113888	3	41	4,3	14,9	267	8,1	0,40		
06-juin-00	16	660666	5112137	3	88	2,4	15,2	249	8,2	0,13		
06-juin-00	17	660245	5111133	4	3	1,8	16,6	202	8,4			
06-juin-00	18	660327	5111052	4	0	1,4	17,0	210	8,5			
06-juin-00	201	657753	5116097	1	108	2,2	15,9	193	7,7	0,16		
07-juin-00	201	658330	5116798	1	108	1,9	15,9	175	7,7	0,14		
19-juin-00	202	661034	5113912	3	41	1,8	16,6	252	7,9			
20-juin-00	201	658330,2	5116798,4	1	108	1,3	18,1	201	7,5			
21-juin-00	1	659307	5117651	1	108	1,7	17,7	198	7,4	0,13		
21-juin-00	2	661953	5118858	2	4	3,2	17,2	213	7,6	0,20		
21-juin-00	3	662432	5120742	1	91	2,5	17,7	197	7,5	0,18		

date	site	X	Y	water	MMB	Zt	Temp	Cond	pH	Courant	MES	A440
21-juin-00	4	664224	5120267	2	2	3,5	17,3	215	7,7	0,31		
21-juin-00	5	665195	5122669	1	60	2,4	17,7	203	7,5	0,15		
21-juin-00	6	668708	5122919	2	11	3,7	17,9	223	7,7	0,27		
21-juin-00	7	670678	5124723	1	18	3,3	17,8	203	7,5	0,32		
21-juin-00	8	673262	5124798	2	10	4,3	17,7	232	7,8	0,28		
21-juin-00	9	675662	5127227	1	16	2,6	18,3	210	7,6	0,25		
21-juin-00	10	677581	5126781	2	0	2,8	17,8	217	7,6	0,21		
21-juin-00	11	677953	5126202	2	0	14,0	17,7	231	7,7	0,30		
21-juin-00	13	668560	5120043	3	0	12,5	16,6	257	7,9			
21-juin-00	14	659086	5114369	3	0	14,6	16,6	256	7,9			
21-juin-00	15	660278	5113809	3	41	2,1	16,6	264	8,1			
21-juin-00	16	660640	5112431	3	88	1,5	16,6	255	8,0	0,08		
21-juin-00	17	660547	5111395	4	3	1,8	18,9	219	7,9	0,36		
04-juil-00	202	661045	5113926	3	41	2,3	20,1		7,9	0,14		
05-juil-00	1	659301	5117628	1	108	2,3	20,3	204	7,4	0,23		
05-juil-00	2	661975	5118899	2	4	3,7	20,3	228	7,5	0,35		
05-juil-00	14	658980	5114297	3	0	14,6	19,9	264	7,8	1,03		
05-juil-00	15	660034	5113977	3	41	2,9	19,2	242	8,5	0,03		
05-juil-00	16	660580	5112456	3	88	2,1	20,3	278	8,3	0,23		
05-juil-00	17	660591	5111217	4	3	1,0	21,8	280	8,0	0,32		
05-juil-00	202	661045	5113926	3	41	2,4						
06-juil-00	201	658330,2	5116798,4	1	108	2,1	20,2	192	7,4	0,14		
18-juil-00	1	659431	5117629	1	108	2,0	21,0	189	7,5	0,15		
18-juil-00	2	661884	5118721	2	4	3,4	20,8	228	7,7	0,26		
18-juil-00	14	659021	5114340	3	0	14,6	20,7	261	8,0	0,94		
18-juil-00	15	660494	5113500	3	41	3,0	20,8	272	8,1	0,25		
18-juil-00	16	660560	5112359	3	88	1,7	21,3	272	8,5	0,03		
18-juil-00	17	660722	5111342	4	3	0,9	21,9	251	7,8	0,21		
19-juil-00	1	659469	5117691	1	108	2,0	20,4	192	7,5	0,16		
19-juil-00	2	661760	5118525	2	4	3,4	20,5	234	7,7	0,27		
19-juil-00	3	662420	5120562	1	91	2,7	20,7	202	7,6	0,16		
19-juil-00	4	664115	5120451	2	2	3,7	20,5	227	7,7	0,31		
19-juil-00	5	665465	5122654	1	60	2,8	20,2	187	7,5	0,15		
19-juil-00	6	668705	5122575	2	11	3,7	20,5	237	7,8	0,26		
19-juil-00	7	670737	5124591	1	18	3,7	20,4	205	7,6	0,35		
19-juil-00	8	673102	5124977	2	10	4,3	20,8	238	7,0	0,33		
19-juil-00	9	676032	5127044	1	16	2,9	20,6	191	7,6	0,30		
19-juil-00	10	677616	5126809	2	0	3,0	20,7	209	7,7	0,25		
19-juil-00	11	677899	5126126	2	0	12,5	20,6	245	7,9	0,35		
19-juil-00	13	668358	5120019	3	0	13,0	20,7	243	8,0			
19-juil-00	14	659017	5114334	3	0	15,2	20,7	272	8,0	0,90		
19-juil-00	19	657460	5113989	2	85	2,8	21,1	242	7,8	0,16		
31-juil-00	202	661058	5113923	3	41	2,0	22,7	245	8,2	0,20		
01-août-00	201	658321	5116814	1	108	1,7	23,1	176	7,5	0,05		
02-août-00	1	659507	5117743	1	108	1,9	22,8	171	7,7	0,11		
02-août-00	2	661922	5118754	2	4	3,4	22,9	203	7,9	0,30		
02-août-00	3	662302	5120936	1	91	2,4	22,9	176	7,7	0,17		
02-août-00	4	664270	5120433	2	2	3,6	23,1	201	7,7	0,36		
02-août-00	5	665320	5123135	1	60	2,2	22,7	176	7,6	0,14		
02-août-00	6	668644	5122709	2	11	3,7	23,0	208	7,8	0,25		
02-août-00	7	670763	5125243	1	18	2,0	23,3	174	7,8	0,50		
02-août-00	8	673109	5124595	2	10	4,3	22,9	212	7,8	0,35		
02-août-00	9	675680	5127636	1	16	2,1	23,6	174	7,7	0,01		

date	site	X	Y	water	MMB	Zt	Temp	Cond	pH	Courant	MES	A440
02-août-00	10	677577	5126839	2	0	2,9	24,0	193	7,6	0,09		
02-août-00	11	677830	5126135	2	0	12,8	23,7	217	7,7	0,09		
02-août-00	13	668358	5120019	3	0	13,1		237				
02-août-00	14	659180	5114490	3	0	14,6	22,8	240	7,6	0,87		
14-août-00	201	658358	5116815	1	108	1,6	23,2	137	7,3	0,09		
15-août-00	202	661053	5113909	3	41	1,9	23,1	233	8,0	0,20		
17-août-00	204	660162	5110810	4	0	1,5	22,9	281	7,8	0,34		
28-août-00	1	659341	5117615	1	108	1,6	20,3	146	7,0	0,12		
28-août-00	2	661839	5118557	2	4	3,3	21,0	196	7,6	0,25		
28-août-00	3	662441	5120675	1	91	2,4	20,5	148	7,5	0,17		
28-août-00	4	664382	5120430	2	2	3,3	21,1	198	8,2	0,32		
28-août-00	5	665897	5122926	1	60	2,3	21,0	163	7,6	0,12		
28-août-00	6	668716	5122549	2	11	3,5	20,9	214	8,1	0,08		
28-août-00	7	670699	5125234	1	18	1,9	21,4	140	7,9	0,02		
28-août-00	8	673236	5124684	2	10	4,3	22,0	249	8,2	0,35		
28-août-00	9	675664	5127644	1	16	2,0	21,6	146	8,1	0,04		
28-août-00	10	677570	5126815	2	0	2,8	21,5	178	7,8	0,20		
28-août-00	11	677959	5126122	2	0	12,8	22,1	254	8,1	0,50		
28-août-00	13	668408	5119999	3	0	12,5	21,8	258	8,1			
28-août-00	14	659104	5114368	3	0	15,2	21,7	260	8,1	0,78		
29-août-00	1	659396	5117579	1	108	1,8	20,7	190	7,6	0,12		
29-août-00	2	661738	5118589	2	4	2,9	21,0	202	7,8	0,28		
29-août-00	14	659015	5114351	3	0	15,2	21,3	253	8,1	0,96		
29-août-00	15	660036	5113514	3	41	1,9	21,3	272	8,3	0,10		
29-août-00	16	660194	5112201	3	88	1.3	21,1	273	8,4	0,10		
29-août-00	17	660282	5110924	4	3	0,8	21,9	223	8,0	0,02		
29-août-00	19	657405	5113565	2	85	2,5	21,2	206	7,8	0,12		
05-sept-00	201	658358	5116812	1	108	1,6	18,8	142	7,5	0,06		
08-sept-00	204	660162	5110810	4	0	0,9	17,8	208	7,7	0,20		
11-sept-00	202	661053	5113909	3	41	1,3	20,5	273	8,0	0,14		
14-sept-00	1	659546	5117915	1	108	1,5	19,5	147	7,6	0,16		
14-sept-00	2	661749	5118653	2	4	2,8	19,5	191	7,9	0,30		
14-sept-00	14	659036	5114192	3	0	15,2	20,5	272	8,2	1,02		
14-sept-00	15	660043	5113640	3	41	1,3	20,3	279	8,3	0,17		
14-sept-00	16	660573	5112352	3	88	1,3	20,3	273	8,3	0,20		
14-sept-00	17	660590	5111373	4	3	0,7	20,0	216	8,0	0,05		
14-sept-00	19	657398	5113660	2	85	2,3	19,9	224	8,0	0,11		
31-oct-00	201	658256	5116309	1	108	1,5	8,6	155	7,5	0,14		
31-oct-00	202	659882	5113224	3	41	1,4	10,4	274	8,2	0,17		
31-oct-00	204	660059	5110763	4	0	1,9	4,6	174	8,0	0,24		
07-mai-01	Q1	658229	5117322	1	54	1,2	11,8	106	7,3	0,02	8,8	0,017
07-mai-01	Q10	653460	5111197	2	emer	1,2	16,0	150	7,6	0,05	3,4	0,012
07-mai-01	Q2	659222	5117726	1	59	2,2	12,4	122	7,3	0,24	9,1	0,015
07-mai-01	Q3	660250	5117783	2	0		12,2	138	7,4	0,33	6,4	0,013
07-mai-01	Q4	658938	5114295	3	0		11,3	220	7,7	0,74	6,0	0,007
07-mai-01	Q5	660004	5114478	3	58		12,0	239	7,8	0,17	2,3	0,004
07-mai-01	Q6	659610	5112993	3	127	2,5	11,2	235	7,7	0,36	6,0	0,004
07-mai-01	Q7	659850	5112144	3	130	2,3	11,2	222	7,8	0,28	6,6	0,004
07-mai-01	Q8	660327	5111270	4	2	2,0	13,2	194	7,9	0,36	12,0	0,011
07-mai-01	Q9	660474	5110685	4	emer	0,8	14,0	130	7,8	0,12	5,3	0,013
08-mai-01	Q4	658938	5114292	3	0		11,8	225	7,7	0,76	6,4	0,006
08-mai-01	Q8	660321	5111197	4	2	2,0	13,6	167	7,8	0,45	10,2	0,011
23-mai-01	Q1	658315	5117317	1	54	0,5	17,1	194	7,9	0,21		

date	site	X	Y	water	MMB	Zt	Temp	Cond	pH	Courant	MES	A440
23-mai-01	Q10	653443	5111180	2	emer	0,5	16,7	204	7,1	0,01	40,5	0,016
23-mai-01	Q2	659441	5117725	1	59	1,4	16,8	204	8,1	0,20	13,2	0,008
23-mai-01	Q3	660252	5117724	2	0	3,0	16,3	209	8,0	0,40	12,2	0,007
23-mai-01	Q4	658938	5114295	3	0		15,3	238	8,1	0,91	4,7	0,005
23-mai-01	Q5	660208	5114629	3	58	2,3	15,4	241	8,3	0,15	5,4	0,004
23-mai-01	Q6	659550	5112939	3	127	1,7	15,1	239	8,2	0,31	4,8	0,004
23-mai-01	Q7	660005	5111865	3	130	1,0	15,2	215	8,2	0,21	7,7	0,004
23-mai-01	Q8	660461	5111172	4	2	0,4	18,2	191	8,6	0,18	11,3	0,010
05-juin-01	Q1	658130	5117071	1	54	0,7	15,9	148	7,2	0,05	8,0	0,014
05-juin-01	Q10	653414	5111138	2	emer	1,0	17,8	178	7,9	0,04	20,5	0,009
05-juin-01	Q2	659287	5117799	1	59	1,7	15,8	155	7,7	0,24	9,0	0,014
05-juin-01	Q3	660308	5117801	2	0	3,4	15,6	158	7,8	0,42	9,4	0,012
05-juin-01	Q4	658940	5114293	3	0		15,0	215	8,1	0,91	6,8	0,006
05-juin-01	Q5	660231	5114759	3	58	3,1	15,0	225	8,3	0,16	3,3	0,004
05-juin-01	Q6	659529	5112982	3	127	1,8	14,9	232	8,2	0,20	5,4	0,004
05-juin-01	Q7	659956	5111845	3	130	1,4	15,1	0	8,1	0,14	6,9	0,004
05-juin-01	Q8	660263	5111245	4	2	1,3	16,7	136	8,2	0,40	24,6	0,013
05-juin-01	Q9	659962	5110110	4	emer	0,7	17,4	279	8,5	0,11	33,6	0,012
18-juin-01	Q1	658288	5116988	1	54	0,5	19,9	129	7,4	0,06	5,0	0,009
18-juin-01	Q10	653433	5111020	2	emer	0,6	27,8	123	8,6	0,02	16,2	0,012
18-juin-01	Q2	659175	5117578	1	59	0,9	20,7	129	7,5	0,15	5,7	0,008
18-juin-01	Q3	660269	5117791	2	0	2,4	21,0	132	7,5	0,38	11,8	0,007
18-juin-01	Q4	658941	5114302	3	0		20,6	140	7,8	0,81	9,7	0,005
18-juin-01	Q5	660243	5114727	3	58	2,2	21,7	138	8,5	0,02	2,0	0,004
18-juin-01	Q6	659465	5112745	3	127	1,3	21,8	138	8,2	0,00	6,0	0,004
18-juin-01	Q7	659856	5112002	3	130	0,8	23,5	134	8,9	0,02	9,5	0,005
18-juin-01	Q8	660256	5111234	4	2	0,6	25,0	121	8,0	0,24	18,9	0,013
18-juin-01	Q9	659961	5110101	4	emer	0,6	24,8	154	8,3	0,00	38,8	0,010
04-juil-01	Q1	658882	5117008	1	54	0,8	19,6	114	7,5	0,08	4,9	0,009
04-juil-01	Q10	653538	5111049	2	emer	0,6	20,8	127	8,7	0,01	28,8	0,009
04-juil-01	Q2	659335	5117538	1	59	1,0	19,7	118	7,3	0,19	5,1	0,008
04-juil-01	Q3	660181	5117759	2	0	2,3	20,3	120	7,5	0,21	8,8	0,008
04-juil-01	Q4	658941	5114302	3	0		19,7	143	7,9	0,97	11,1	0,004
04-juil-01	Q5	660366	5114844	3	58	2,4	19,7	149	8,4	0,00	2,0	0,003
04-juil-01	Q6	659340	5112565	3	127	1,3	21,5	144	8,7	0,00	5,2	0,003
04-juil-01	Q7	659679	5112116	3	130	1,2	21,2	142	9,1	0,00	4,2	0,003
04-juil-01	Q8	660139	5111190	4	2	0,9	19,4	148	7,6	0,33	19,6	0,014
04-juil-01	Q9	659965	5110087	4	emer	0,5	20,4	230	7,9	0,01	46,3	0,019
17-juil-01	Q1	658606	5116575	1	54	1,2	20,1	112	7,3	0,00	21,8	0,016
16-juil-01	Q10	653689	5111081	2	emer	0,5	20,3	128	7,1	0,00	4,9	0,008
17-juil-01	Q2	659384	5117793	1	59	1,2	20,4	116	7,4	0,08	16,7	0,012
17-juil-01	Q3	660280	5117785	2	0	2,8	20,6	119	7,5	0,32	9,7	0,009
16-juil-01	Q4	658941	5114302	3	0		20,0	153	7,8	0,84	6,4	0,004
17-juil-01	Q5	660244	5114727	3	58	2,4	19,8	163	7,7	0,00	2,8	0,003
16-juil-01	Q6	659474	5112740	3	127	1,5	20,7	161	8,3	0,00	2,8	0,003
16-juil-01	Q7	659771	5111827	3	130	1,0	20,0	163	8,2	0,03	2,8	0,004
16-juil-01	Q8	660062	5111074	4	2	1,4	21,2	135	7,5	0,41	43,6	0,019
16-juil-01	Q9	659971	5110107	4	emer	0,6	21,0	273	7,4	0,10	68,4	0,033
30-juil-01	Q1	658507	5117015	1	54	0,7	23,3	123	9,1	0,00	8,2	0,009
30-juil-01	Q10	653667	5111043	2	emer	1,0	26,7	138	8,7	0,00	0,7	0,006
30-juil-01	Q2	659032	5117494	1	59	0,7	22,7	125	9,2	0,00	10,7	0,009
30-juil-01	Q3	660110	5117826	2	0	2,0	23,0	130	7,9	0,28	5,8	0,007
30-juil-01	Q4	658941	5114302	3	0		22,7	157	8,2	0,78	7,2	0,003
30-juil-01	Q5	660195	5114709	3	58	2,3	23,0	165	8,4	0,20	5,7	0,003
30-juil-01	Q6	659480	5112986	3	127	1,1	23,1	165	8,5	0,04	4,3	0,003
30-juil-01	Q7	659904	5111891	3	130	0,7	23,9	157	9,0	0,00	7,4	0,003
30-juil-01	Q8	660181	5111368	4	2	1,3	23,9	158	8,4	0,30	27,3	0,014
30-juil-01	Q9	660183	5110991	4	emer	0,5	25,6	184	8,7	0,00	41,5	0,013
13-août-01	Q1	658592	5116561	1	54	0,9	24,5	224	8,3	0,01	21,1	0,010

date	site	X	Y	water	MMB	Zt	Temp	Cond	pH	Courant	MES	A440
14-août-01	Q1	658814	5116806	1	54	0,7	21,6	202	9,1	0,00	3,1	0,009
14-août-01	Q10	653670	5111038	2	emer	0,7	25,5	230	8,5	0,00	1,9	0,006
14-août-01	Q2	659222	5117595	1	59	0,8	22,0	210	8,4	0,04	7,0	0,011
14-août-01	Q3	660286	5117765	2	0	2,4	24,0	235	7,8	0,23	9,3	0,005
14-août-01	Q4	658941	5114302	3	0		23,9	266	8,1	0,83	7,8	0,003
13-août-01	Q5	660248	5114733	3	58	2,1	23,8	281	8,0	0,28		
14-août-01	Q5	660261	5114785	3	58	2,2	23,4	277	8,1	0,22	10,9	0,003
13-août-01	Q6	659476	5112744	3	127	1,0	24,0	280	8,1	0,09	6,0	0,002
14-août-01	Q6	659558	5112753	3	127	1,2	23,8	276	8,2	0,05	6,4	0,002
13-août-01	Q7	659905	5112254	3	130	0,9	23,9	279	8,0	0,04		
14-août-01	Q7	659831	5112177	3	130	0,7	24,0	273	8,2	0,00	13,6	0,003
14-août-01	Q8	660015	5111325	4	2	0,8	23,9	267	8,1	0,28	12,1	0,004
14-août-01	Q9	659970	5110074	4	emer	0,5	25,0	300	8,0	0,00	31,8	0,015
14-août-01	Q9B			4	0		25,6	253	8,1			
27-août-01	Q1	658603	5116560	1	54	1,0	21,0	162	7,2	0,03	12,9	0,012
27-août-01	Q10	653572	5111054	2	emer	0,4	21,4	384	6,9	0,00	2,0	0,008
27-août-01	Q2	659276	5117570	1	59	1,1	21,4	164	7,3	0,05	11,8	0,011
27-août-01	Q3	660276	5117801	2	0	2,4	22,1	185	7,6	0,28	6,6	0,006
27-août-01	Q4	658941	5114302	3	0		22,7	235	8,0	0,79	7,0	0,003
27-août-01	Q5	660249	5114736	3	58	2,2	22,6	237	8,1	0,22	24,3	0,003
28-août-01	Q6	659525	5112950	3	127	1,1	22,6	235	8,0	0,09	7,5	0,002
28-août-01	Q7	659919	5111693	3	130	0,8	21,1	231	7,6	0,08	4,0	0,002
28-août-01	Q8	660136	5111007	4	2	0,9	22,2	232	7,8	0,25	21,7	0,012
28-août-01	Q9	659961	5109995	4	emer	0,4	21,3	259	7,8	0,04	35,2	0,012
28-août-01	Q9B	660145	5109996	4	0	1,7	22,2	229	7,7	0,05	21,6	0,012
11-sept-01	Q1	658702	5116698	1	54	0,9	19,6	131	7,1	0,06	13,4	0,014
10-sept-01	Q10	653920	5111124	2	emer	0,7	21,6	212	7,6	0,00	5,2	0,006
11-sept-01	Q2	659714	5117746	1	59	0,9	20,5	135	7,3	0,04	12,4	0,010
11-sept-01	Q3	660250	5117785	2	0	2,2	21,6	145	7,4	0,30	12,6	0,009
11-sept-01	Q4	658940	5114294	3	0		22,2	213	8,0	0,85	5,4	0,003
10-sept-01	Q5	660257	5114778	3	58	2,4	22,4	227	8,1	0,31	6,6	0,002
10-sept-01	Q6	659461	5112732	3	127	1,2	22,2	228	8,1	0,03	4,0	0,002
10-sept-01	Q7	659931	5111869	3	130	0,6	21,8	223	8,2	0,00	2,3	0,003
10-sept-01	Q8	660140	5111113	4	2	0,9	22,8	227	8,0	0,31	32,8	0,017
10-sept-01	Q9	659966	5110083	4	emer	0,6	22,0	265	8,1	0,06	36,8	0,016
10-sept-01	Q9B	660101	5110124	4	0	2,1	23,5	173	7,9	0,07	22,8	0,012
24-sept-01	Q1	658194	5116864	1	54	0,7	18,7	149	7,5	0,04	4,1	0,013
24-sept-01	Q10	653883	5111120	2	emer	0,8	20,1	239	8,3	0,00	2,2	0,007
24-sept-01	Q2	659271	5117727	1	59	1,2	19,1	161	7,5	0,08	3,3	0,010
24-sept-01	Q3	660250	5117744	2	0	2,8	19,1	165	7,3	0,40	4,1	0,009
24-sept-01	Q4	658948	5114295	3	0		19,8	280	7,7	0,92	5,0	0,003
24-sept-01	Q5	660210	5114662	3	58	2,1	19,8	290	7,9	0,28	2,0	0,002
24-sept-01	Q6	659592	5112946	3	127	1,3	19,7	289	7,9	0,15	3,2	0,002
24-sept-01	Q7	660034	5111958	3	130	0,9	19,4	285	8,0	0,09	2,2	0,002
24-sept-01	Q8	660315	5111385	4	2	1,4	18,7	285	7,8	0,31	19,4	0,010
24-sept-01	Q9	659958	5110085	4	emer	0,5	18,4	308	8,0	0,00	29,2	0,011
24-sept-01	Q9B	660119	5110088	4	0	2,1	18,4	255	7,4	0,11	16,6	0,013
10-oct-01	Q1			1	54	0,6	12,0	119	7,0	0,11		
10-oct-01	Q10			2	emer	0,6	10,9	231	6,9	0,00	2,8	0,007
10-oct-01	Q10b			2	emer		11,3	206	7,0		1,6	0,006
10-oct-01	Q2			1	59	1,1	11,9	119	7,0	0,10	16,6	0,016
10-oct-01	Q3			2	0	2,4	12,5	125	7,0	0,40	10,0	0,015
10-oct-01	Q4			3	0		13,6	249	7,5	0,91	6,7	0,004
10-oct-01	Q5			3	58	2,5	13,5	274	7,6	0,17	3,7	0,003
10-oct-01	Q6			3	127	2,0	13,6	272	7,6		5,5	0,002
10-oct-01	Q7			3	130	0,8	13,2	274	7,6	0,05	9,2	0,003
10-oct-01	Q8			4	2	0,7	11,0	314	7,5	0,33	19,6	0,015
10-oct-01	Q9			4	emer	0,3	11,7	336	7,5	0,00	28,8	0,013
10-oct-01	Q9B			4	0	1,7	10,1	289	7,3	0,08	14,0	0,017
22-oct-01	Q1	658536	5117222	1	54	0,7	10,9	110	6,9	0,07	6,8	0,019
22-oct-01	Q10	653759	5111105	2	emer	0,5	9,0	204	6,7	0,00	5,3	0,013

date	site	X	Y	water	MMB	Zt	Temp	Cond	pH	Courant	MES	A440
22-oct-01	Q2	659202	5117781	1	59	1,1	10,7	111	6,9	0,13	7,2	0,018
22-oct-01	Q3	660285	5117875	2	0	2,5	10,9	119	7,0	0,44	13,4	0,016
22-oct-01	Q4	658947	5114305	3	0		12,1	236	7,4	0,80	7,3	0,006
22-oct-01	Q5	660288	5114754	3	58	2,4	12,2	274	7,7	0,15	7,0	0,003
22-oct-01	Q6	659527	5112981	3	127	1,5	12,2	274	7,6		4,3	0,002
22-oct-01	Q7	659917	5111840	3	130	1,0	12,0	272	7,7	0,15	3,5	0,003
22-oct-01	Q8	660204	5111130	4	2	0,9	10,1	314	7,8	0,29	12,9	0,012
22-oct-01	Q9	659951	5110086	4	emer	0,5	10,2	346	8,0	0,01	31,3	0,009
22-oct-01	Q9B	660139	5110030	4	0	2,0	9,8	292	7,8	0,07	9,0	0,014

		Ktotal							Phyto	Macrophytes		Epiphytes		Biomasse		
date	site	moy	sd	n	type	Kwater	Kplant	zplant	(Chla)	Subm	Emer	zsam	plant	moy	sd	N
04-mai-00	14	0,79		1	1	0,79			0,7	0						
04-mai-00	23	1,80		1	1	1,80			1,9	0						
04-mai-00	24	1,00		1	1	1,00			0,9	0						
04-mai-00	25	0,90	0,06	2	1	0,90			0,9	0						
04-mai-00	26	0,80		1	1	0,80				0						
04-mai-00	27	2,60		1	1	2,60			15,6	0						
04-mai-00	28	1,52		1	1	1,52			4,6	0						
11-mai-00	201								2,5	0						
11-mai-00	202								1,2	0						
22-mai-00	1	2,32	0,03	4	1	2,32			2,8	0						
22-mai-00	2	1,64	0,09	4	1	1,64			1,8	0						
22-mai-00	3	2,16	0,04	5	1	2,16			2,8	0						
22-mai-00	4	1,59	0,07	5	1	1,59			1,7	0						
22-mai-00	5	2,14	0,03	5	1	2,14			2,6	0						
22-mai-00	6	1,57	0,04	5	1	1,57			1,6	0						
22-mai-00	7	1,89	0,08	4	1	1,89			2,0	0						
22-mai-00	8	1,51	0,03	4	1	1,51			1,6	0						
22-mai-00	9	2,06	0,01	4	1	2,06			1,9	0						
22-mai-00	10	1,73	0,06	5	1	1,73			1,9	0						
22-mai-00	11	1,58	0,01	3	1	1,58			2,1	0						
22-mai-00	12	1,10	0,06	3	1	1,10			1,5	0						
22-mai-00	13	1,09	0,05	3	1	1,09			1,5	0						
22-mai-00	14	1,22	0,01	3	1	1,22			1,6	0						
22-mai-00	15	1,17	0,07	3	1	1,17			1,6	0						
22-mai-00	16	1,26	0,01	4	1	1,26			2,6	0						
22-mai-00	17	2,09	0,16	3	1	2,09			4,9	0						
22-mai-00	18	2,71	0,18	3	1	2,71			6,5	0						
23-mai-00	1	2,17	0,07	4	1	2,17			3,0	0						
23-mai-00	2	1,65	0,03	4	1	1,65			2,4	0						
23-mai-00	3	2,00	0,03	4	1	2,00			3,0	0						
23-mai-00	4	1,58	0,05	4	1	1,58			2,2	0						
23-mai-00	15	1,01	0,05	4	1	1,01			1,7	0						
23-mai-00	16	1,16	0,02	4	1	1,16			2,4	1						
23-mai-00	20	1,16	0,04	3	1	1,16			1,6	0						
23-mai-00	21	1,11	0,05	3	1	1,11			1,5	0						
23-mai-00	22	2,41	0,02	4	1	2,41			7,0	0						
23-mai-00	202	1,21	0,03	3	1	1,21			1,6	0						
05-juin-00	202	1,01	0,05	3	1	1,01			1,9	1						
06-juin-00	1	1,67		1	1	1,67			3,4	0						
06-juin-00	2	1,47	0,01	3	1	1,47			2,8	0						
06-juin-00	3	1,88	0,02	4	1	1,88			3,8	1						
06-juin-00	4	1,60	0,13	4	1	1,60			2,6	0						
06-juin-00	5	1,74	0,07	3	1	1,74			3,5	1						
06-juin-00	6	1,36	0,08	4	1	1,36			2,3	0						
06-juin-00	7	1,88	0,09	4	1	1,88			4,1	0						
06-juin-00	8	1,39	0,15	3	1	1,39			2,3	0						
06-juin-00	9	1,73	0,13	3	1	1,73			4,9	0						
06-juin-00	11	1,39	0,07	3	1	1,39			2,7	0						
06-juin-00	13	1,22	0,06	2	1	1,22			2,5	0						
06-juin-00	14	1,03	0,05	3	1	1,03			2,5	0						
06-juin-00	15	0,89	0,05	4	1	0,89			2,8	0						
06-juin-00	16	0,97	0,07	3	1	0,97			2,9	0						
06-juin-00	17	1,98	0,11	3	1	1,98			10,6	0						
06-juin-00	18	2,04	0,18	4	1	2,04			11,3	0						
06-juin-00	201									1						
07-juin-00	201	2,06	0,14	7	2				3,4	1		1,5	POTR	168	57	6
19-juin-00	202	1,22	0,01	4	1	1,22			2,9	1						
20-juin-00	201	1,73	0,11	5	2				3,5	1		0,1	POTR	647	760	6
										1		1,2	VALA	225	168	5
21-juin-00	1	1,51	0,03	5	2				3,2	1						
21-juin-00	2	1,32	0,05	5	1	1,32			2,5	1						
21-juin-00	3	1,56	0,08	4	1	1,56			2,7	1						
21-juin-00	4	1,31	0,03	4	1	1,31			2,7	0						
21-juin-00	5	1,37	0,05	4	1	1,37			3,2	0						

		Ktotal							Phyto	Macrophytes		Epiphytes		Biomasse		
date	site	moy	sd	n	type	Kwater	Kplant	zplant	(Chla)	Subm	Emer	zsam	plant	moy	sd	N
21-juin-00	6	1,10	0,05	4	1	1,10			2,4	0						
21-juin-00	7	1,60	0,07	4	1	1,60			3,7	0						
21-juin-00	8	1,09	0,02	4	1	1,09			1,9	0						
21-juin-00	9	1,47	0,07	4	1	1,47			3,8	0						
21-juin-00	10	1,31	0,05	4	1	1,31			3,7	0						
21-juin-00	11	1,14	0,06	3	1	1,14			2,7	0						
21-juin-00	13	1,04	0,01	3	1	1,04			2,3	0						
21-juin-00	14	0,98	0,03	3	1	0,98			2,6	0						
21-juin-00	15	2,93	0,04	2	2				3,8	1		0,1	POTP	844	141	2
										1		0,1	POTR	79	43	2
21-juin-00	16	1,77			2	0,67	3,43	0.9-1.5	5,0	1						
21-juin-00	17	1,87	0,07	4	1	1,87			12,8	0						
04-juil-00	202	1,04	0,04	4	1	1,04			2,2	1		2,1	VALA	250	107	6
05-juil-00	1	2,33	0,07	5	2				2,3	1		1,9	VAL/POTR	81	22	6
05-juil-00	2	2,05	0,10	4	1	2,05			2,0	1						
05-juil-00	14	1,27	0,08	4	1	1,27			1,2	0						
05-juil-00	15	2,87	0,23	5	2				3,4	1		0,3	POTP	980	300	6
05-juil-00	16	1,89	0,33	4	2				2,3	1		0,1	POTP	4946	1023	6
05-juil-00	17	2,52	0,18	4	1	2,52			18,2	0						
05-juil-00	202								2,0	1						
06-juil-00	201	3,24	0,31	5	2				1,9	1		0,2	POTR	120	57	6
										1		1,8	VALA	129	19	6
18-juil-00	1	1,72	0,04	4	2				2,2	1		1	POTR	194	0	1
										1		1,6	VALA	74	17	5
18-juil-00	2	1,31	0,02	4	1	1,31			2,3	1		3,3	VALA	48	6	6
18-juil-00	14	1,02	0,06	3	1	1,02			1,7	0						
18-juil-00	15	0,84	0,03	4	1	0,84			1,7	1		2,8	VALA	188	57	6
18-juil-00	16	1,77	0,24	4	2				2,8	1		0,1	POTP	1922	1188	6
18-juil-00	17	2,08	0,13	4	1	2,08			7,1	1		0,8	VALA	278	57	6
19-juil-00	1	2,11	0,20	3	2				2,6	1		1,5	VALA	109	33	6
19-juil-00	2	1,49	0,01	3	1	1,49			2,2	1		3,1	VALA	54	6	6
19-juil-00	3	1,74	0,07	4	1	1,74			2,6	1		2,5	VALA	58	12	6
19-juil-00	4	1,35	0,04	3	1	1,35			2,3	1						
19-juil-00	5	1,73	0,09	3	2				2,1	1		1,3	)TR/VALA+AA1	393	164	2
										1		2,6	VALA	48	6	4
19-juil-00	6	1,06	0,05	3	1	1,06			1,7	1						
19-juil-00	7	1,69	0,01	3	1	1,69			2,0	0						
19-juil-00	8	1,13	0,14	3	1	1,13			2,1	1						
19-juil-00	9	1,90	0,05	3	1	1,90			2,9	0						
19-juil-00	10	1,67	0,14	3	1	1,67			3,4	1		2,8	VALA	60	21	6
19-juil-00	11	1,13	0,14	3	1	1,13			2,8	0						
19-juil-00	13	0,99	0,09	3	1	0,99			2,2	0						
19-juil-00	14	0,95	0,05	3	1	0,95			2,3	0						
19-juil-00	19	1,42	0,07	3	1	1,42				1		2,4	VALA	248	51	6
31-juil-00	202	0,93	0,13	5	2				2,2	1		1,3	VAL/HET	459	289	6
01-août-00	201	2,62	0,33	4	2				4,5	1		1,2	VALA	1664	437	3
										1		0,1	POTR	328	138	3
02-août-00	1	1,98	0,18	4	2				2,1	1		1,5	VALA	3406	1819	5
										1		1,3	POTR	3139	0	1
02-août-00	2	1,32	0,05	3	1	1,32			1,3							
02-août-00	3	1,28	0,03	3	2				1,9	1		1,7	VALA	1304	311	3
										1		1,7	POTR	132	7	3
02-août-00	4	1,19	0,04	3	1	1,19			1,0	1						
02-août-00	5	1,12	0,05	4	2				2,1	1		1,9	VALA	3125	842	4
										1		1,9	POTR	1137	369	2
02-août-00	6	0,92	0,01	3	1	0,92			1,0	1		3,5	VALA	45	8	6
02-août-00	7	1,35	0,14	4	2				2,3	1		1,4	VALA	3193	1237	4
										1		1,4	POTR/VAL	1024	529	2
02-août-00	8	0,84	0,03	3	1	0,84			1,3	0						
02-août-00	9	2,81			2	1,43	5,00	0-2.1	3,0	1		1,6	VALA	1857	648	2
										1		0,1	POTR	169	73	4
02-août-00	10	1,09	0,01	3	1	1,09			2,1	1						
02-août-00	11	0,86	0,07	3	1	0,86			1,2	0						
02-août-00	13								1,2	0						

		Ktotal							Phyto	Macrophytes		Epiphytes		Biomasse		
date	site	moy	sd	n	type	Kwater	Kplant	zplant	(Chla)	Subm	Emer	zsam	plant	moy	sd	N
02-août-00	14	0,84	0,06	3	1	0,84			1,3	0						
14-août-00	201	2,83			2	1,85	4,47	1-1.6	2,0	1		1,1	VALA	436	68	6
										1		0,2	POTR	100	0	1
15-août-00	202	2,66			2	1,05	4,68	1-1.8	1,5	1		1,1	VALA/HETD	237	203	6
17-août-00	204	5,30	0,51	5	1	5,30			21,9	0						
28-août-00	1	2,44	0,15	4	2				1,8	1		1,2	VALA	1736	920	6
28-août-00	2	1,54	0,07	4	1	1,54			1,4	1		3,1	VALA	284	26	6
28-août-00	3	2,08	0,07	4	1	2,08			1,4	1						
28-août-00	4	1,42	0,07	3	1	1,42			1,4	1						
28-août-00	5	1,54	0,05	4	2				1,6	1		1,8	VALA	420	136	6
28-août-00	6	1,27	0,03	4	1	1,27			7,9	1		3,3	VALA	158	24	5
28-août-00	7	1,60	0,13	4	2				3,3	1		1,8	POTR	187	26	3
										1		1,6	VALA	972	199	3
28-août-00	8	0,90	0,01	3	1	0,90			3,5	0						
28-août-00	9	3,37			2	1,24	9,08	0-2	3,7	1		1,6	VALA	985	298	3
										1		0,1	POTR	736	639	6
28-août-00	10	1,11	0,07	4	1	1,11			2,0	1		2,6	VALA	411	210	3
28-août-00	11	0,93	0,03	3	1	0,93			1,2	0						
28-août-00	13	0,92	0,03	3	1	0,92			0,9	0						
28-août-00	14	0,85	0,03	3	1	0,85			1,0	0						
29-août-00	1	2,62	0,31	4	2				2,3	1		1,4	VALA	1528	938	4
										1		1,4	POTR	453	206	2
29-août-00	2	1,44	0,21	4	2				1,6	1		2,7	VALA	537	114	6
29-août-00	14	1,03	0,05	3	1	1,03			0,8	0						
29-août-00	15	1,76			2	1,04	4,97	1.2-1.9	1,1	1		1,6	VALA	2125	821	6
29-août-00	16	1,29	0,27	4	2				1,7	1		0,8	VALA	2496	1349	6
29-août-00	17	4,44	1,25	4	2				12,7	1		0,1	VALA	144	5	2
										1		0,1	POTR	249	113	4
29-août-00	19	1,28	0,10	4	2		5,51	2-2.5	1,8	1		2	VALA	2104	444	6
										1		2	NIT	1092	29	2
05-sept-00	201	2,37	0,21	4	2				2,0	1		1,3	VALA	788	379	6
08-sept-00	204	2,50	0,16	3	1	2,50			14,9	0						
11-sept-00	202	2,74			2	0,92	5,66	0.8-1.3	1,2	1		0,8	VALA	794	216	6
14-sept-00	1	2,43	0,24	6	2				1,2	1		1,4	VALA	405	174	6
14-sept-00	2	1,24	0,04	4	1	1,24			1,0	1		2,6	VALA	475	164	6
14-sept-00	14	0,77	0,04	3	1	0,77			0,6	0						
14-sept-00	15	1,01			2	0,91			0,8	1		1,2	VALA	1651	443	6
14-sept-00	16	1,43			2	1,19	6,58	0.8-1.2	1,3	1		1	VALA	1460	328	6
14-sept-00	17	3,85	1,00	4	2	3,85			11,2	1		0,1	POTR	111	65	6
14-sept-00	19	1,51			2	1,25	4,76	2-2.3	1,4	1		1,8	NIT	679	83	2
										1		1,3	VALA	2393	601	3
										1		1,1	POTR	631	396	3
31-oct-00	201	1,72	0,05	3	1	1,72			1,4	0						
31-oct-00	202	0,82	0,19	3	1	0,82			1,4	0						
31-oct-00	204	1,79	0,27	3	1	1,79			3,3	0						
07-mai-01	Q1	2,80	0,43	4	1	2,80			2,3	0	1	0,1	TYPA	234	190	5
07-mai-01	Q10	1,55	0,24	5	1	1,55			4,2	0	1	0,1	SPAE	1214	1640	5
07-mai-01	Q2	2,05	0,10	3	1	2,05			2,6	0						
07-mai-01	Q3	1,77	0,02	3	1	1,77			2,4	0						
07-mai-01	Q4	0,91	0,02	3	1	0,91			1,2	0						
07-mai-01	Q5	0,84	0,04	3	1	0,84			0,7	0						
07-mai-01	Q6	0,83	0,06	3	1	0,83			1,1	0						
07-mai-01	Q7	0,91	0,01	3	1	0,91			1,4	0						
07-mai-01	Q8	1,84	0,05	3	1	1,84			11,5	0						
07-mai-01	Q9	2,15	0,57	7	1	2,15			7,6	0	1	0,1	SCIL	323	172	5
08-mai-01	Q4	0,98	0,04	3	1	0,98			1,4	0						
08-mai-01	Q8	1,99	0,05	3	1	1,99			12,3	0						
23-mai-01	Q1	6,21	0,81	4	1	6,21				0	1	0,1	SPAE	896	873	4
23-mai-01	Q10	6,13	2,81	6	1	6,13			18,2	0	1	0,1	TYPA	50	22	4
23-mai-01	Q2	1,86	0,13	3	1	1,86			5,9	0						
23-mai-01	Q3	1,67	0,09	3	1	1,67			4,8	0						
23-mai-01	Q4	0,86	0,02	3	1	0,86			2,4	0						
23-mai-01	Q5	0,94	0,05	3	1	0,94			2,7	0						
23-mai-01	Q6	0,93	0,07	3	1	0,93			2,5	0						

		Ktotal							Phyto	Macrophytes		Epiphytes		Biomasse		
date	site	moy	sd	n	type	Kwater	Kplant	zplant	(Chla)	Subm	Emer	zsam	plant	moy	sd	N
23-mai-01	Q7	0,91	0,06	3	1	0,91			3,3	0						
23-mai-01	Q8	2,18	0,50	3	1	2,18			16,4	0						
05-juin-01	Q1	2,28	0,14	5	1	2,28			2,7	1	1	0,1	TYPA	484	328	4
05-juin-01	Q10	4,19	2,17	5	1	4,19			29,2	1	1	0,1	TYPA	33	9	4
05-juin-01	Q2	1,99	0,05	5	1	1,99			2,6	0						
05-juin-01	Q3	1,68	0,04	3	1	1,68				0						
05-juin-01	Q4	1,00	0,03	3	1	1,00			1,9	0						
05-juin-01	Q5	1,08	0,05	3	1	1,08			1,8	1						
05-juin-01	Q6	0,85	0,09	3	1	0,85			2,2	1						
05-juin-01	Q7	0,93	0,03	3	1	0,93			2,1	1						
05-juin-01	Q8	2,45	0,07	3	1	2,45			25,0	0						
05-juin-01	Q9	4,02	0,15	5	1	4,02			45,7	1	1	0,1	SCIL	513	144	4
18-juin-01	Q1	1,38	0,22	5	2				2,7	1		0,1	POTR	1817	1058	3
											1	0,1	SCIL	333	116	3
18-juin-01	Q10	3,70	0,72	5	3		3,70		10,4	0	1	0,1	SCIL	235	52	4
18-juin-01	Q2	1,30	0,05	5	1	1,30			3,4	1						
18-juin-01	Q3	1,47	0,00	4	1	1,47			4,5	0						
18-juin-01	Q4	1,06	0,03	3	1	1,06			2,4	0						
18-juin-01	Q5	1,69	0,06	5	3		1,69		2,0	1		0,1	POTP	386	67	4
18-juin-01	Q6	3,03			2	1,04	3,82		3,7	1		0,1	POTP	1197	302	5
18-juin-01	Q7	2,87			2	1,27	3,84		5,6	1		0,1	POTP	1550	728	5
18-juin-01	Q8	2,48	0,03	3	1	2,48			15,5	0						
18-juin-01	Q9	9,89	2,52	5	3		9,89		25,5	1		0,1	POTR/VALA	95	19	3
											1	0,1	SCIL	57	18	3
04-juil-01	Q1	1,68	0,20	6	2				5,4	1		0,6	VALA/POTR	5582	6478	3
											1	0,1	SCIL	82	62	3
04-juil-01	Q10	1,42	0,21	5	2				4,6	1		0,1	HETD	622	138	3
											1	0,1	SCIL	35	6	3
04-juil-01	Q2	1,49	0,25	5	2		5,73	0.5-1	3,1	1		0,8	VALA	1365	594	4
04-juil-01	Q3	1,39	0,06	5	1	1,39			2,6	0						
04-juil-01	Q4	1,03	0,06	3	1	1,03			1,6	0						
04-juil-01	Q5	1,83	0,12	5	2				1,9	1		0,1	POTP	55	31	4
04-juil-01	Q6	2,54	0,44	4	2				5,7	1		0,1	POTP	3246	4130	5
04-juil-01	Q7	1,65	0,25	5	2				4,2	1		0,1	POTP	390	113	4
04-juil-01	Q8	2,52	0,05	3	1	2,52			17,7	0						
04-juil-01	Q9	11,35	3,43	3	3	5,02	11,35		47,7	1		0,1	VALA/POTR	3347	1249	3
											1	0,1	SCIL	169	90	3
17-juil-01	Q1	4,06	0,85	5	2				5,4	1		0,1	POTR	637	386	3
										1		1	VALA	763	366	3
											1	0,1	TYPA	87	117	3
16-juil-01	Q10	2,10	0,25	6	2				2,8	1		0,1	HETD	345	275	3
											1	0,1	SCIL	46	4	3
17-juil-01	Q2	2,40			2	1,79			5,0	1		0,1	POTR	3548	5258	3
										1		1	VALA	462	212	3
17-juil-01	Q3	1,70	0,04	5	1	1,70			3,0	0						
16-juil-01	Q4	0,82	0,05	3	1	0,82			1,3	0						
17-juil-01	Q5	3,32	0,96	5	2					1		0,1	POTP	2114	909	5
16-juil-01	Q6	2,86	0,39	5	2					1		0,1	POTP	2776	2220	4
16-juil-01	Q7	2,61			2	1,00	3,57			1		0,1	POTR	947	192	4
16-juil-01	Q8	4,23	0,19	3	1	4,23			11,3	0						
16-juil-01	Q9	10,10	1,83	5	3	3,57	10,10		15,0	1		0,1	POTR	297	95	3
											1	0,1	SCIL	75	11	3
30-juil-01	Q1	3,08	0,73	4	2				0,7	1		0,1	VALA	1371	1030	3
											1	0,1	SCIL	823	669	3
30-juil-01	Q10	2,88	0,80	5	2				2,0	1		0,1	ELO CAN	195	116	3
											1	0,1	SPAE	46	23	3
30-juil-01	Q2	3,68	1,44	5	2				6,7	1		0,1	POTR	1256	454	3
										1		0,1	VALA	1468	649	3
30-juil-01	Q3	1,33	0,08	3	1	1,33			4,3	0						
30-juil-01	Q4	0,83	0,02	4	1	0,83			1,5	0						
30-juil-01	Q5	1,02	0,05	5	1	1,02			3,1	0						
30-juil-01	Q6	4,68				1,01	11,10	0.7-1.1	3,2	1		0,7	VALA	3416	2876	5
30-juil-01	Q7	1,78			2	0,72	3,89		5,6	1		0,2	VALA	5447	3738	5
30-juil-01	Q8	3,10	0,24	3	1	3,10			22,5	0						

		Ktotal							Phyto	Macrophytes		Epiphytes		Biomasse		
date	site	moy	sd	n	type	Kwater	Kplant	zplant	(Chla)	Subm	Emer	zsam	plant	moy	sd	N
30-juil-01	Q9	16,04	5,22	3	3	6,53	16,04		34,5	1		0,1	POTR	182	41	3
											1	0,1	TYPA	41	21	3
13-août-01	Q1								3,2	1		0,25	VALA	245	170	4
14-août-01	Q1	4,18	0,89	5	2				0,9	1		0,25	VALA	470	169	3
											1	0,2	SCIL	81	39	3
14-août-01	Q10	5,38			2	2,98	7,18		6,1	1		0,1	.OC/VALA/MYI	613	331	3
											1	0,1	SPAE	105	68	3
14-août-01	Q2	3,11	0,88	6	2				2,0	1		0,2	VALA	481	531	4
14-août-01	Q3	1,56	0,12	5	1	1,56			4,3	0						
14-août-01	Q4	0,98	0,01	3	1	0,98			1,2	0						
13-août-01	Q5									0						
14-août-01	Q5	1,78	0,26	5	1	1,78			2,7	0						
13-août-01	Q6								1,7	1		0,15	HETD	233	46	4
14-août-01	Q6	2,77			2	1,12	3,64		1,5	1						
13-août-01	Q7									1		0,15	VALA	65	29	4
14-août-01	Q7	2,75			2	1,91	3,59		2,5	1						
14-août-01	Q8	1,18	0,16	5	1	1,18			3,2	0						
14-août-01	Q9	9,47	1,86	3	3	3,93	9,47		11,4	1		0,1	VALA	131	49	3
											1	0,1	SCIL	23	7	3
14-août-01	Q9B									0						
27-août-01	Q1	2,84	0,23	5	2				3,7	1		0,4	VALA	188	109	3
											1	0,1	TYPA	53	45	3
27-août-01	Q10	3,48			2	1,34	5,63		4,0	1		0,1	HETD	106	27	3
											1	0,1	SPAE	16	11	3
27-août-01	Q2	5,22	1,26	5	2				2,9	1		0,8	VALA	466	415	3
27-août-01	Q3	1,30	0,05	2	1	1,30			2,9	0						
27-août-01	Q4	0,89	0,02	3	1	0,89			1,1	0						
27-août-01	Q5	1,96	0,07	3	1	1,96			1,7	0						
28-août-01	Q6	2,42			2	0,85	4,00		1,5	1		0,8	VALA	748	409	5
28-août-01	Q7	2,71			2	0,86	4,55		1,9	1		0,5	VALA	154	35	4
28-août-01	Q8	3,12	0,10	3	1	3,12			8,8	0						
28-août-01	Q9	14,78	1,72	3	3	4,10	14,78		11,1	1		0,1	VALA	240	53	3
											1	0,1	SCIL	97	46	3
28-août-01	Q9B	2,72	0,03	3	1	2,72			8,5	0						
11-sept-01	Q1	3,72	0,56	5	2				2,4	1		0,2	VALA	576	466	3
											1	0,1	TYPA	44	17	3
10-sept-01	Q10	5,67			2	0,96	8,82		2,9	1		0,15	CERD/ELOC	118	42	3
											1	0,1	SCIL	11	5	3
11-sept-01	Q2	3,31			2	2,51	4,11		2,6	1		0,2	VALA	118	20	3
										1		0,1	POTR	120	11	3
11-sept-01	Q3	1,79	0,10	3	1	1,79			2,3	0						
11-sept-01	Q4	0,86	0,02	3	1	0,86			1,3	0						
10-sept-01	Q5	1,01	0,21	3	1	1,01			1,3	0						
10-sept-01	Q6	2,45			2	0,86	4,05		1,4	1		0,45	VALA	811	163	5
10-sept-01	Q7	3,58			2	1,03	6,13		2,5	1		0,2	VALA	464	86	5
10-sept-01	Q8	4,29	0,33	3	1	4,29			27,2	0						
10-sept-01	Q9	12,78	1,84	3	3	5,20	12,78		41,2	1		0,1	VALA	102	54	3
												0,1	SCIL	79	32	3
10-sept-01	Q9B	3,08	0,12	3	1	3,08			6,9	0						
24-sept-01	Q1	1,63	0,12	6	2	1,33			1,4	1		0,5	VALA	5757	4162	3
											1	0,1	SCIL	154	247	3
24-sept-01	Q10	4,42			2	1,31	6,29	0.3-0.8	6,5	1		0,2	ELOC	166	26	3
											1	0,1	SCIL	29	12	3
24-sept-01	Q2	2,96			2	1,27	3,80		1,4	1		0,5	VALA	152	96	3
24-sept-01	Q3	1,54	0,15	3	1	1,54			1,4	0						
24-sept-01	Q4	0,77	0,05	3	1	0,77			0,8	0						
24-sept-01	Q5	0,51	0,14	3	1	0,51			1,1	0						
24-sept-01	Q6	3,46			2	1,05	4,97	0.5-1.3	1,1	1		0,6	VALA	1384	1119	4
24-sept-01	Q7	4,76			2	1,05	9,41	0.5-0.9	1,2	1		0,6	VALA	615	233	4
24-sept-01	Q8	2,58	0,04	3	1	2,58			10,3	0						
24-sept-01	Q9	5,30	0,95	6	2				23,3	1		0,2	VALA	334	41	3
											1	0,1	TYPA	71	26	3
24-sept-01	Q9B	2,66	0,03	3	1	2,66			4,8	0						
10-oct-01	Q1	6,39	0,40	3	1	6,39				0	1	0,1	SCIL	25	4	3

		Ktotal							Phyto	Macrophytes		Epiphytes		Biomasse		
date	site	moy	sd	n	type	Kwater	Kplant	zplant	(Chla)	Subm	Emer	zsam	plant	moy	sd	N
10-oct-01	Q10	9,27	2,48	3	3	4,07	9,27		7,0	1		0,1	MYRS	100	11	3
											1	0,1	SCIL	26	8	3
10-oct-01	Q10b	1,11	0,21	4	1	1,11			4,1	0						
10-oct-01	Q2	2,35	0,06	3	1	2,35			2,4	1			VALA	128	15	3
10-oct-01	Q3	1,97	0,08	3	1	1,97			1,4	0						
10-oct-01	Q4	0,95	0,07	3	1	0,95			0,9	0						
10-oct-01	Q5	0,79	0,11	3	1	0,79			1,8	0						
10-oct-01	Q6	2,53			2	0,85	4,22	1.0-2.0	1,6	1			HETD	151	42	3
10-oct-01	Q7	1,66			2	1,10	5,63	0.5-0.8	4,6	1			VALA	553	148	4
10-oct-01	Q8	2,86	0,44	4	1	2,86			8,2	0						
10-oct-01	Q9	4,40			3	4,14	9,33		14,8	1		0,1	MYRS	637	380	3
											1	0,1	SCIL	90	12	3
10-oct-01	Q9B	2,36	0,04	3	1	2,36			3,2	0						
22-oct-01	Q1	2,28	0,20	3	1	2,28			1,2	0	1	0,1	SCIL	8	2	3
22-oct-01	Q10	2,44	0,14	3	1	2,44			4,0	1		0,25	MYRS	82	19	3
											1	0,1	SCIL	6	1	3
22-oct-01	Q2	2,44	0,14	3	1	2,44			1,4	1			VALA	131	10	2
22-oct-01	Q3	2,14	0,03	3	1	2,14			1,4	0						
22-oct-01	Q4	0,90	0,08	3	1	0,90			1,2	0						
22-oct-01	Q5	0,86	0,10	3	1	0,86			1,3	0						
22-oct-01	Q6	0,95	0,11	5	1	0,95			1,1	1			VALA	526	92	3
22-oct-01	Q7	2,10			2	0,89	3,44	0.5-0.95	2,1	1			VALA	244	75	3
22-oct-01	Q8	3,51	0,88	3	1	3,51			24,3	0						
22-oct-01	Q9	3,07	0,11	6	1	3,07			48,0	0	1	0,1	SCIL/TYPA	58	12	4
22-oct-01	Q9B	2,06	0,09	3	1	2,06			5,1	0						