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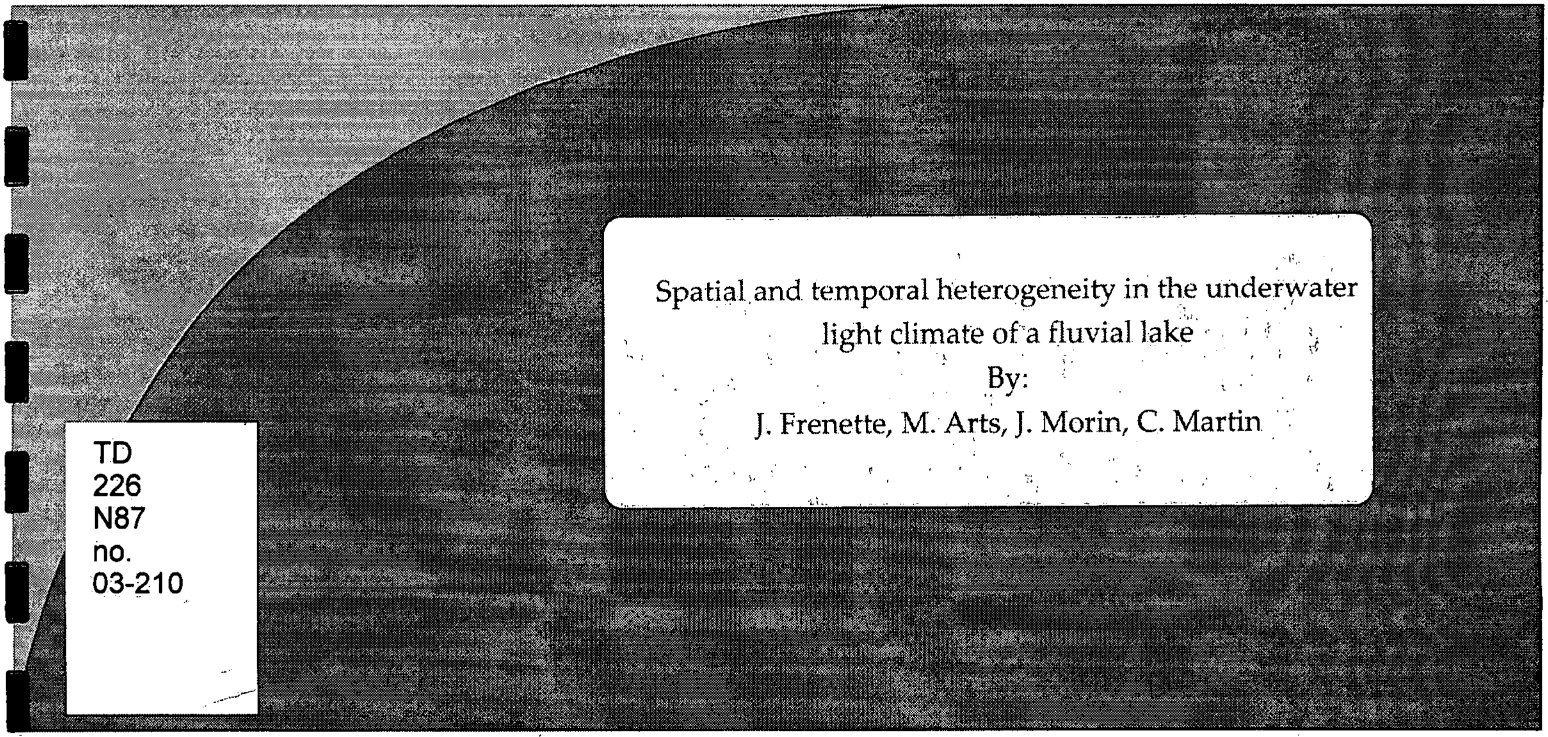

Spatial and temporal heterogeneity in the underwater light climate of a fluvial lake

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03-210

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Running head: Light climate in a fluvial lake

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NWRI Contribution # 03-210

Keywords: Fluvial lake, transport time, spatial heterogeneity, underwater light climate, UV radiation

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Abstract

Fluvial lakes are hydro-dynamically complex systems which share characteristics of both lentic and lotic systems. The challenge, for limnologists, is to understand how this unique combination of lentic and lotic influences interacts with landscape-driven processes to produce the complex spatial and temporal mosaic of physico-chemical environments typical of such lakes.

We measured characteristics of the underwater light spectra (e.g. attenuation of ultraviolet radiation [UVR], photosynthetically active radiation [PAR]) and select dissolved and particulate physico-chemical properties (e.g. particulate organic carbon [POC], chlorophyll *a*) in the different water masses of Lake Saint-Pierre (Quebec, Canada). We used these variables as tracers to reveal the extent and magnitude of spatial and temporal heterogeneity in key optical and chemical parameters characteristic of this large, shallow, and hydro-dynamically complex fluvial lake. Our analysis of spectral components of the different water masses integrates the effects of seasonal changes in water levels, light-attenuating chemicals (e.g. CDOM) and suspended particles and highlights the large spectral heterogeneity in underwater conditions that may be encountered in fluvial lakes.

We also demonstrate the utility of bio-optical approaches in defining the magnitude of site-to-site variation in both the vertical and horizontal dimension. We present a new way to present the optical and chemical variable data; one that is based on transport time rather than distance from source tributaries. This new presentation method will provide researchers with a tool to more accurately model the effect of downstream processes (e.g. microbial degradation, UV photolysis) and connectivity on key chemical variables in fluvial lakes and rivers.

Hétérogénéité spatiale et temporelle dans le régime de lumière sous-marin d'un lac fluvial

Jean-Jacques Frenette, Michael T. Arts, Jean Morin et Carl Martin

Résumé

Les lacs fluviaux sont des réseaux hydrodynamiques complexes qui combinent les caractéristiques des systèmes lentiques et lotiques. Pour les limnologues, le défi consiste à comprendre comment cette combinaison unique d'influences lentiques et lotiques interagit avec des processus régis par la morphologie du milieu, de manière à produire une mosaïque spatiale et temporelle complexe de milieux physicochimiques typiques de ces lacs.

Nous avons mesuré les caractéristiques du spectre lumineux sous-marin (p. ex. l'atténuation du rayonnement ultraviolet [UV], le rayonnement à action photosynthétique [RAP]) et certaines propriétés physicochimiques des matières dissoutes et des particules (p. ex. le carbone organique particulaire [COP] et la chlorophylle *a*) dans différentes masses d'eau du lac St-Pierre (Québec, Canada). Nous avons utilisé ces variables comme traceurs pour déterminer l'étendue et l'ampleur de l'hétérogénéité spatiale et temporelle de caractéristiques clés des paramètres optiques et chimiques de ce lac fluvial étendu et peu profond, à caractéristiques hydrodynamiques complexes. Notre analyse des éléments spectraux des différentes masses d'eau tient compte des effets des changements saisonniers des niveaux d'eau, des composés chimiques qui atténuent la lumière (p. ex. les matières organiques dissoutes colorées) et des particules en suspension, et elle met en évidence la grande hétérogénéité spectrale des conditions sous-marines qu'on peut observer dans les lacs fluviaux.

Nous démontrons également l'utilité des approches biooptiques pour déterminer l'ampleur des variations d'un site à l'autre, verticalement et horizontalement, et nous faisons la démonstration d'une nouvelle façon de présenter les variables optiques et chimiques, fondée sur le temps de transport plutôt que sur la distance des tributaires. Cette nouvelle méthode de présentation offre aux chercheurs un outil supplémentaire qui leur permet de modéliser avec précision les effets des processus en aval (p. ex. la dégradation des agents microbiens, la photolyse UV), ainsi que les rapports entre des variables chimiques clés dans les lacs fluviaux et les cours d'eau.

NWRI RESEARCH SUMMARY

Plain language title

Variability, in space and time, in underwater light fields of a fluvial lake.

What is the problem and what do sicentists already know about it?

Measurements of water quality are usually made at one or, at most, a few stations in a lake often incorporating an integrated water sampling strategy which attempts to take into account the two dimensional (vertical) stratification typical of temperate lakes. Such a sampling strategy may be wholly inappropriate for fluvial lakes because they are extremely dynamic with respect to the distribution of their water masses; each of which may be quite variable in terms of its physico-chemical characteristics.

Why did NWRI do this study?

We used select underwater light climate variables (attenuation coefficients, absorbance of particulates) and several additional parameters (e.g. dissolved organic carbon [DOC], chlorophyll, particulates etc) as a proxies of other water quality measures to demonstrate the extreme variability inherent in the physico-chemical properties of the different water masses of a typical fluvial lake in space and time.

What were the results?

We developed a new way to express the spatial-temporal variability in the above parameters which captures information on the residence time of the individual water masses as they pass down the lake. This portrayal allowed us to examine, in a more realistic way, the effects of downstream processes (e.g. photodegradation, extra-cellular release of DOC by macrophytes) on key physico-chemical variables in the lake.

How will these results be used?

Lake Saint-Pierre is the largest fluvial lake (~400 km^2) of the St.-Lawrence river ecosystem, one of the three largest rivers in North America. Lake Saint-Pierre has recently been classified by UNESCO as an "*Ecological Reserve of the Biosphere*" and is now officially recognized as a world heritage site. This recognition arose, in part, because of its high biodiversity; the lake supports 83 fish species and 288 bird species. It is a very productive and unique ecosystem characterized by a variety of habitats including; extensive wetlands (6,900 ha), embayments, shallow and deep lotic sections that differ greatly in their residence times and numerous incoming tributaries with diverse physico-chemical characteristics. Because of this complexity it is a useful "proving ground" for satellite monitoring research programs. Our data thus serve to ground-truth planned future monitoring from space. Our study also demonstrates that water quality sampling strategies must explicitly recognize the distinct spatial variability in the distribution of the water masses of fluvial lakes in general. In addition, our results explain why commercial fisheries located along the south shore are more productive and reinforces the application of management strategies focused more specifically on this region of the lake. Finally, we suggest that the extreme heterogeneity in habitats and physico-chemical parameters in the different water masses of Lake Saint-Pierre are the underlying reason why this ecological reserve of the biosphere has such high biological diversity.

Who were our main partners in the study?

University of Quebec in Trois Rivieres

Sommaire des recherches de l'INRE

Titre en langage clair

Variabilité, dans le temps et dans l'espace, des champs lumineux sous-marins d'un lac fluvial.

Quel est le problème et que savent les chercheurs à ce sujet?

Les mesures de la qualité de l'eau sont habituellement prises à une seule station (ou quelques stations tout au plus) et comportent souvent une méthode d'échantillonnage de l'eau qui tient compte de la stratification bidimensionnelle (verticale) typique des lacs tempérés. Une telle méthode d'échantillonnage s'avère souvent inadéquate dans les lacs fluviaux puisque ceux-ci sont très dynamiques par rapport à la distribution de leurs masses d'eau; or ces dernières peuvent avoir des caractéristiques physico-chimiques très différentes.

Pourquoi l'INRE a-t-il effectué cette étude?

Diverses variables de l'environnement lumineux sous-marin (coefficients d'atténuation, absorbance des particules) ainsi que plusieurs autres paramètres (p. ex. carbone organique dissous [COD], chlorophylle, matières particulaires, etc.) ont été utilisés en tant qu'approximations d'autres mesures de la qualité de l'eau afin de démontrer l'extrême variabilité spatio-temporelle des propriétés physico-chimiques des différentes masses d'eau d'un lac fluvial.

Quels sont les résultats?

Pour exprimer la variabilité spatio-temporelle des paramètres précités, nous avons élaboré une nouvelle méthode qui tient compte des renseignements sur le temps de séjour des masses d'eau pendant leur déplacement. Ces informations ponctuelles nous ont permis d'étudier de façon concrète les effets des processus qui se déroulent en aval (p. ex. photodégradation, émission extracellulaire de COD par des macrophytes) sur d'importantes variables physico-chimiques du lac.

Comment ces résultats seront-ils utilisés?

Le lac Saint-Pierre est le plus important lac fluvial (~400 km^2) de l'écosystème du fleuve Saint-Laurent, un des trois grands fleuves en Amérique du Nord. Récemment, le lac Saint-Pierre a été désigné réserve de la biosphère par l'UNESCO et est maintenant reconnu en tant que site patrimonial mondial. Cette reconnaissance résulte en partie de sa grande biodiversité : le lac abrite 83 espèces de poissons et 288 espèces d'oiseaux. Il s'agit là d'un écosystème unique et très productif, caractérisé par la variété de ses habitats : grandes étendues de milieux humides (6 900 ha), baies, milieux lotiques de différentes profondeurs et dont les temps de séjour varient grandement, nombreux affluents avec différentes caractéristiques physico-chimiques. Toutes ces conditions en font une zone d'essai très utile pour les programmes de surveillance par satellite. Nos données servent ainsi à valider les futurs programmes de surveillance par télédétection. Notre étude montre aussi que les méthodes d'échantillonnage pour l'analyse de la qualité de l'eau doivent tenir compte de façon explicite de la variabilité spatiale dans la distribution des masses d'eau dans tout lac fluvial. De plus, les résultats obtenus permettent de comprendre pourquoi les pêcheries commerciales le long de la rive sud du lac sont plus productives et ils viennent appuyer la mise en œuvre de stratégies de gestion axées sur cette partie du lac en particulier. Finalement, nous avançons que la très grande diversité biologique de cette réserve de la biosphère s'explique par l'extrême diversité des habitats et par les paramètres physico-chimiques des différentes masses d'eau du lac Saint-Pierre.

Quels étaient nos principaux partenaires dans cette étude?

Université du Québec à Trois-Rivières

Introduction

Nature is organized along three spatial dimensions; a fact which contributes to its complexity. Traditionally, however, studies which examine the physical, chemical and biological processes occurring within lake ecosystems have been applied mostly in two dimensions i.e. with emphasis on bivariate combinations of physical, chemical and biological variables over time; but especially with depth (Kalff 2002). Such processes include changes in light attenuation, vertical distributions of plankton components and predators which are all strongly influenced by the stratification (epi-, meta- and hypo-limnion) and/or mixing regimes within the water column (Horne and Goldman 1994).

This "vertical paradigm" has been applied with success to the pelagic (offshore) zone of lakes on the basis that this area is the most representative portion of the lake (in terms of volume), despite the pre-eminent importance of the littoral zone (in terms of productivity) (Wetzel 2001). This may, in part, explain why shallow littoral stations are typically under-sampled compared to deep stations even though they are the most productive regions in lakes. Actually, large differences in underwater light climate have been documented between inshore and offshore regions of lakes (Frenette and Vincent, 2003). This horizontal (i.e. inshore-offshore) heterogeneity is further accentuated in fluvial lakes which are essentially hybrids between lakes and rivers and thus do not conform to the traditional vertical paradigm espoused by researchers of lake ecosystems (Horne and Goldman 1994; Kalff, 2002; Wetzel 2001). This heterogeneity is even more pronounced in fluvial lakes that have multiple inflows, which can result in the formation of chemically and spectrally distinct water masses within the lake (Frenette et al., 2003). In fluvial lakes with large width/depth ratios such water masses can persist and may exhibit very little lateral mixing downstream (Frenette et al., 2003). The establishment of such distinct water masses, in the case of fluvial lakes, confers a unique pattern of primarily horizontal, rather than vertical, stratification as in lakes.

Deep-water zones of lakes are generally much less affected by nearshore macrophytes and/or wind-driven particle re-suspension from the bottom. Fluvial lakes, however, are generally characterized by a relatively large biomass of submerged macrophyte and are also affected by wind-induced mixing regimes that can further modify characteristics of their internal water masses through sediment resuspension (Scheffer 1998). Despite such observations, water quality monitoring strategies in fluvial lakes and other lakes in general typically emphasize sampling at offshore sites even though such locations inadequately represent the primary sites of water quality impacts and concerns (Frenette and Vincent, 2003).

Lotic ecosystems are characterized by multidimensional environmental gradients. These spatial (and temporal) patterns directly affect ecological processes which ultimately translates into variations in biodiversity, productivity (Wiens 2002 and refs therein) and stability of ecosystems (Huxel and McCann, 1998). For example, the river discharge determines the degree of connectivity i.e. the level of exchange of matter, organisms and energy between habitats (Tockner et al. 2000 and refs therein). Longitudinal patterns in habitat variables along the course of rivers have served as a central theme in stream ecology but much less attention have been given to the lateral dimension (Ward and Tockner 2001); a critical dimension in temperate flood plain systems such as fluvial lakes. Recent studies have shown that lateral transfers of materials between habitats may be responsible for specific trophic level responses which in turn affect stability and resilience of ecosystems (Polis et al. 1997; Huxel and McCann 1998). Biotic communities, in turn, will respond in complex and inter-dependant ways to downstream and localized changes in lateral, vertical and longitudinal connectivity.

Few data are available however to address the topic of river landscape heterogeneity in river-floodplain systems such as fluvial lakes which are characterized by distinct patterns of expansion and contraction or to analyze temporal changes in temporal heterogeneity at the floodplain-scale in response to fluctuating discharge. Various patterns of physicochemical variables (e.g. NO_3, specific conductance, shoreline index etc) have been used to characterize the degree of connectivity or spatial heterogeneity or physical complexity between habitats (Refs in Poole 2002). However, since ecosystem behavior is strongly affected by changes in matter and energy (Lindeman 1942), the degree of connectivity between habitats should also be driven by changes in underwater light environments. Underwater solar radiation has many documented, pivotal, roles in photochemistry and photobiology, for example, for primary production of phytoplankton, periphyton and macrophytes and for vision and behavior of adult and larval fish (e.g.

Seehausen et al. 1997; Job and Bellwood, 2000). Underwater light can also operate in subtle ways, for example, by modulating algal stoichiometry and lipid composition which, in turn, has implications for food quality and nutrient transfers to higher trophic levels (Rai et al. 1997, Sterner and Elser 2002; Frenette et al. 1998). Given that light is fundamental for photosynthesis it is somewhat surprising that spatial heterogeneity in underwater light climate has been so poorly studied in most aquatic systems.

Complexity in fluvial lakes is further enhanced by differences in current velocity (transport time) amongst water masses. Transport time within each of the water masses is affected by discharge of the individual tributaries, friction generated by macrophytes, proximity to shore, depth, slope and morphology of the river bed (Morin et al. 2000b). These differences in transport time interact with the inherent chemical characteristics of the different water masses to affect productivity of fluvial lakes through differential changes in light (UV) exposure.

We document the spatial and temporal variability in underwater light climate in a hydro-dynamically complex fluvial lake (Lake Saint-Pierre) located within the St. Lawrence River. We characterize heterogeneity in underwater light climate amongst the four main water masses in this lake. In doing so, we provide detailed empirical field data that defines the range of variation of selected optical and chemical characteristics of the water masses in both space and time. Downstream changes in bio-optical and chemical signals were examined in original way, i.e. by relating these variables to downstream transport time using 2D hydrodynamic simulations for spatial integration instead of to the more usual linear distance from the incoming tributary. This new approach provides a more realistic way to portray underwater light [UV] attenuation to researchers interested in downstream processes (e.g. photo-oxidation and/or microbial degradation of DOC) and how such processes will influence microbial productivity and diversity. Finally, we discuss and explore the implications of this spatio-temporal heterogeneity to provide a structural framework for the high biodiversity associated with this lake, in particular, and, fluvial lakes in general.

Methods

Study site – Lake Saint-Pierre (lat: 46°12'; long: 72°50') is the largest (315 km^2) fluvial lake along the St. Lawrence River and the last major enlargement (13.1 km width at mean discharge) of the river before the St. Lawrence estuary. Lake Saint-Pierre is shallow (mean depth of 3.17 m during the period of mean discharge) and covered with extensive macrophyte beds during summer. It has a large width/depth ratio and, it is this feature that is principally responsible for the limited lateral mixing within the lake's water masses (Frenette et al. 1989; Frenette et al. 2003). Briefly, the lake can be broadly divided into three areas (hereafter referred to as the north, central and south zones). These three areas are composed of inflows (water masses) from the; a) Ottawa, Du Loup, and Maskinongé Rivers, b) St. Lawrence River (maritime channel), and, c) Richelieu, Saint-François and Yamaska Rivers, respectively, representing waters characteristic of the Canadian Shield in the North, Laurentian Great Lakes in the west, and agriculturally influenced waters in the south, respectively (Fig. 1a to d). The three areas vary broadly in their concentrations of dissolved and particulate organic and inorganic suspended matter. The north zone is characterized by brown-colored water rich in suspended particles and relatively high dissolved organic carbon (DOC) concentrations derived from humic and fulvic acids originating from podzoils of the northern watersheds (Primeau 1996; Bobée et al. 1977). The central water zone (maritime shipping channel) is composed of "green water" originating from the Great Lakes and is characterized by relatively low DOC and suspended particle concentrations (Cossa et al. 1998). The south zone is characterized by relatively high DOC and low suspended particle concentrations. We focus our analyses on the four major water masses (arising from the Great Lakes, Ottawa, Richelieu and Saint-François tributaries) of Lake Saint-Pierre.

Modeling water mass distributions – The modeling of water mass distributions allows us to identify where stations were located within each water mass during each sampling period (Table 1). We visited between 25 and 30 sampling stations in 2001 situated along three north-south transects located perpendicular to the main east-west axis of Lake Saint-Pierre (roughly 9 stations per transect) on June 8, 27, July 18 and August 13 (Fig. 1a-d). The exact station locations were fixed using a digital Global Positioning System with ±2 m accuracy. By design we positioned stations in each of water mass even as the physical locations (distributions) of the water masses changed seasonally. Hence, the exact locations of sampling stations shifted (Fig. 1a to d; Table 2) somewhat over time.

Currents and water levels were calculated with a 2D hydrodynamic model (horizontal). The HYDROSIM model (Heniche et al. 1999) uses a discretisation of the shallow water equations solved by the finite elements method. The model uses the conservative form of the quantity of movement from the Saint-Venant equations and takes into account spatial patterns of friction associated with the local substratum. The methodology used for the hydrodynamic simulation is similar to Morin et al. (2000a) with inflows at the upper boundary and an imposed water level at the downstream boundary. The finite element mesh used comprised a total of 80,000 elements and 114,000 nodes and covers the entire area from the Port of Montréal to Trois-Rivières (located immediately downstream of Lake Saint-Pierre). The inflows considered in this model correspond to discharges of the major tributaries on each of the sampling dates (Table 2). Bottom friction was parameterized using substratum maps while friction from aquatic plants used in the hydrodynamic model changed spatially and temporally in relation with seasonal plants growth. A similar methodology applied to other part of the St. Lawrence River, is described in Morin et al. (2000b).

Hydrodynamic results were then used as input data into DISPERSIM, an eulerian transport-diffusion model, which uses a finite element resolution scheme (Secretan et al. 2000; Padilla et al. 1997). Lateral mixing was calibrated using data from a dye injection study (INRS-Eau 1991). This dye experiment, and the corresponding model calibration, was done with a discharge of 9150 $m^3 \cdot s^{-1}$. Limits between any two water masses were defined and positioned at points where the concentrations of both water masses were at 50% of their unmixed state. Conductivity measurements taken on each sampling period gave us a further signal ("ground-truthing") to verify the predictions (station locations within each water mass) made by the HYDROSIM and DISPERSIM models.

Calculation of transport time

The stream line function is a well know technique for visualization of particle's path in a hydrodynamic field (Merzkirch 1974). As the hydrodynamic simulations of Lake Saint-

Pierre are at steady state, the stream line function can be used to estimate a particle's path and the transport time between two points on the same stream line. Several stream lines joining two stations located on the same path were extracted and used to calculate the mean velocity and total distance traveled on the particle path. The total distance divided by mean velocity gives total transport time between 2 stations. This transport time was calculated for 8 to 5 stream lines across the entire Lake Saint-Pierre for the 4 sampling dates.

UVR, PAR, beam attenuation and temperature profiles - A spectroradiometer (Model PUV-2545, Biospherical Instruments, San Diego, USA) was used to measure the cosine-corrected downwelling underwater irradiance (E_d) at 313, 320, 340, 443, and 550 nm and downwelling cosine-corrected PAR (400-700 nm). The PUV-2545 was equipped with a C star transmissiometer (Wet Labs inc), 25 cm path length, $\lambda = 488$ nm for measurement of underwater particle attenuation (scattering and absorption). The instruments were slowly lowered through the whole water column at each station and more than 100 measurements$\cdot$m^{-1} were recorded on a portable computer. Light data were corrected by subtracting "dark irradiance" values (obtained when the instrument was fitted with a light-tight neoprene cap at in situ temperatures) from $E_d(\lambda)$ readings. Diffuse vertical attenuation coefficients (K_d) were calculated by linear regression of the natural logarithm of E_d versus depth. The depth to which 1% of subsurface irradiance penetrated ($Z_{1\%}$) was calculated as $4.605/K_d$ (Kirk 1994). Transmittance values (Tr) were converted into beam attenuation (c in cm-1) according to the following formula:

$$c = -1/x \cdot \ln(Tr)$$

Within the photic zone, beam attenuation coefficients (c) at 0.5 m were calculated from smoothed values and averaged from the non-smoothed values for the whole water column.

Mean temperatures, recorded simultaneously with the spectral data, were averaged from depth profiles conducted through the whole water column. The water column was generally well-mixed and exhibited very little if any thermal stratification (data not shown).

Inorganic and organic dry mass - Water samples were filtered on previously combusted (450°C for 4 h) and weighed (W_1) (0.1 mg precision, Mettler Teledo balance model AB104) 25 mm Millipore (GF/F) glass fiber filters. Filters were stored frozen (–20°C) for 2 to 6 months until analysis. Filters were then heated at 60°C for 24 h and placed in a dessicator until dry at which point they were weighed (W_2). The filters were then combusted at 450°C for 16 h and weighed again (W_3).

Where: W_1 = mass of pre-combusted filter
W_2 = mass of organic + inorganic + pre-combusted filter
W_3 = mass of inorganic + pre-combusted filter

Thus:
Organic dry mass = W_2-W_3
Inorganic dry mass = W_3-W_1

POC, CDOM, DOC and aP measurements - Particulate organic carbon (POC) determinations were made on duplicate sub-surface (~40 cm) water samples filtered onto pre-combusted 25 mm GF/F filters. The GF/F filters were stored frozen (-20°C) until POC concentrations could be measured on a Perkin-Elmer CHN analyzer (Model 2400). The CDOM (chromophoric dissolved organic matter) absorption spectra of Millipore glass fiber (0.22 µm) filtered water samples were measured at every nm from 290 to 750 nm using a 1 cm pathlength quartz cuvette in a spectrophotometer (Shimadzu, UV-2401PC) referenced against 0.22 µm membrane-filtered Milli-Q® water and corrected for turbidity absorption at 690 nm (Laurion et al., 2000). For each sample, three measurements were made and averaged. Values were zeroed with Milli-Q water blank as a reference. The turbidity corrected absorption at 340 nm is here defined as *a*CDOM. DOC was analysis using high temperature catalytic oxidation on a Dohrmann DC-190 Total Carbon Analyzer or a Shimadzu TOC 5000A instrument. Both instruments quantify CO_2 released by combustion using a non-dispersive infrared detector calibrated daily with potassium hydrogen phthalate. Filtered water samples were acidified with 20% phosphoric acid and purged for 5 min with the instrument's carrier gas, zero air or oxygen, to remove dissolved inorganic carbon prior to injection for DOC determination (also called NPOC for non-purgeable organic carbon). All determinations were corrected for the system blank, estimated daily by regressing the results of low concentration standards (0, 2, 5 mg $C \cdot L^{-1}$) analyzed as samples, against their "true" value. The system blank corrects for a combination of blank sources internal to the instruments and also residual carbon in the reagent water used to make standards.

For particulate absorption coefficients (*a*P), water samples were vacuum filtered in duplicates through a 25 mm GF/F filter (Whatman), and filters were then stored in the dark at –20°C until measurements of spectral absorption by particulate matter using the quantitative filter technique (QFT). The absorbance of particles concentrated onto filters was measured every 2 nm over the spectral range 320-820 nm according to Roesler (1998) using a Shimadzu UV-2401 PC equipped with an integrating sphere (model ISR-2200). Absorbance values at 500 nm were converted to particulate absorption coefficients (*a*P) using the algorithm of Roesler (1998).

Numerical analysis - Multiple regression analysis was performed using UVA attenuation (K_{d340}) as a dependant variable and CDOM, Chl*a*, POC, *a*P and inorganic dry weight as explanatory variables. The (squared) semi-partial correlations were calculated with Systat (SPSS Inc., Chicago, Il, USA) to express the unique contribution of CDOM, Chl*a*, POC, *a*P, inorganic dry weight to the total variance of K_{d340} (Tabachnick and Fidell, 2001).

To relate spectral composition of the water (Kd 313, 340, 443 and PAR) to environmental variables, we used redundancy analysis (RDA; CANOCO v. 4, ter Braak 1998), a linear eigenvector ordination technique designed for direct analysis of relationship between multivariate data sets (ter Braak 1987, ter Braak and Prentice 1988). RDA was chosen because the range of the ordination sample scores in a detrended correspondence analysis (DCA) with detrending by segments and non-linear rescaling was less than 1.5 standard deviation units (Rodriguez et al 1993), indicating that the use of a linear method was appropriate. Sampling date was included as a covariable to account for possible seasonal trends during summer 2001. Significance test for model relating spectral composition to environmental variables were based on Monte Carlo permutation test (1000 permutations) for the sum of all eigenvalues. Variables entering the final model were selected by a stepwise procedure available in CANOCO program. Selected environmental variables had inflation factors <10, indicating weak covariation between them. Ellipses in Fig. 10 are centered on sample mean of the x and y axes (Systat v.10).

Results

Spatial and temporal distribution of water masses - The relative distributions of water masses changed seasonally (Figs. 1a to d). One of the most prominent features was that the relative contribution (surface area and volume) of the Saint-François River diminished whereas the contribution made by the St. Lawrence River (Great Lakes water) increased over time (Fig. 1a to d). These shifts in water mass distributions were due to changes in relative discharge of the four main tributaries relative to that of the St. Lawrence River (Table 2).

Water level fluctuations in Lake Saint-Pierre - Water levels in Lake Saint-Pierre are mainly a function of the discharge from the St. Lawrence River combined with discharges from its many tributaries. During the summer of 2001, water levels were very low in comparison with the inter-annual mean (Fig.1). For all sampling days the level was 40, 60 and 80 cm lower than the inter-annual mean on June 8th, June 27th and July 18th, and August 13th, respectively. Such periods of low discharge are mainly associated with a very low supply of water from the Great Lakes (Morin and Bouchard 2000).

Transport times - Transport times of the Saint-François water mass were the longest (5-7 d) of all the water masses in Lake Saint-Pierre, the fastest being waters from the Great Lakes (1.5-2.5 d). Intermediary values were found in the Ottawa and Richelieu rivers (3-5.5 d and 2-4 d, respectively). Values were generally lower at the beginning of the summer with a gradual decrease thereafter (Figs. 2-5). We were not able to unequivocally locate enough stations in the Saint-François and Richelieu water masses within Lake Saint Pierre on August 13 and July 18, respectively, primarily because of low discharges of the respective source tributaries on those two dates (Table 2).

Spatial and temporal heterogeneity in inherent optical and chemical characteristics

a) *North-south patterns* –

A comparison of some key optical and chemical parameters of the four main water masses in three transects (upstream, middle and downstream) reveals how the physical-chemical composition of incoming tributaries interacts with within-lake processes to produce a complex and highly dynamic mosaic of underwater light climates in Lake Saint-Pierre (Figs. 2-5). In June, when water levels are high (Table 1), and submerged macrophyte growth is starting (Morin et al. 2000) one can observe, most clearly, the effect of the incoming tributaries (Figs 2 & 3). The penetration of both UV-B and UV-A radiation as well as PAR is highest in the Great Lakes water mass and generally lowest in the water mass originating from the Saint-François River. These patterns are generally well matched to spatial patterns of DOC and CDOM (Frenette et al. 2003). In the Ottawa River water mass CDOM made up a consistently large fraction of total DOC (Figs. 2-5). The concentration of Chl-a and, to some extent, POC was generally lowest in the Great Lakes water mass in June.

In July and August, when discharge of the three smaller tributaries were much lower (Table 1), water levels were sometimes insufficient to allow us to make good depth profiles of underwater light climates or else we could not unequivocally determine whether a given station belonged to a specific water mass. This occurred for stations located in the Saint-François and Richelieu Rivers derived water masses (Figs. 4 & 5). Nevertheless, seasonal changes are once again apparent. For example, attenuation of UV-B, UV-A radiation and PAR on July 18 increased compared to June 27 in the Saint-François and Ottawa water masses (Figs. 3 & 4). This was primarily due to higher DOC and CDOM concentrations in July. Finally, in August when macrophyte abundance/biomass was high, UVR and PAR attenuation as well as DOC and CDOM concentrations were again reduced compared to July.

b) *Upstream-downstream patterns* –

Expressing inherent optical and chemical variables as a function of transport time offers a unique perspective on downstream processes affecting the main water masses in Lake Saint-Pierre. Each water mass exhibited marked changes in its inherent optical and chemical properties through its passage down the lake (Figs. 6-8) These changes are most apparent in the South (i.e. Saint-François and Richelieu Rivers) and North (Ottawa river) zones with general trend of increasing UV and PAR penetration downstream of the source tributaries (Fig. 6). There was no pronounced trend (either increasing or decreasing) in Kd_{313} or Kd_{340} amongst the four sampling dates in the Great Lakes water mass however PAR penetration increased abruptly when the Great Lakes water first enters Lake Saint-Pierre (Fig. 6).

Not surprisingly, upstream-downstream patterns in DOC and $a\mathrm{CDOM}_{340}$ were similar within each water mass (Fig. 7). However, each water mass exhibited its own unique downstream pattern in relative loss or gain of DOC and $a\mathrm{CDOM}_{340}$. In the Saint-François water mass both parameters generally decreased downstream whereas in the Richelieu water mass they increased especially on the first sampling period. There was little fluctuation in either parameter in the Great Lakes water mass. In the Ottawa water mass both DOC and $a\mathrm{CDOM}_{340}$ decreased rapidly from the mouth of the tributary to the first sampling station downstream but stayed relatively constant thereafter. Early summer DOC and corresponding $a\mathrm{CDOM}_{340}$ values were generally higher than later in the season in all four water masses. The absorbance due to particulate matter (*a*P) in the Saint-François, Great Lakes and Ottawa water masses followed a similar pattern to DOC and $a\mathrm{CDOM}_{340}$ (Fig. 8). In the Saint-François, Richelieu and Ottawa water masses *a*P decreased rapidly after their waters entered the lake and then decreased more slowly suggesting that particles were progressively settling downstream.

The load of inorganic dry weight was, predictably, highest in early summer following spring runoff even in the rapidly flowing Great Lakes water mass (Fig. 8). Although the amplitude of fluctuations were more muted in subsequent sampling periods, the overall trend in downstream trajectories in dry weight of inorganic material paralleled that of *a*P (see Fig. 7). Chlorophyll *a* concentrations in the Saint-François water mass were highest and most variable during the first sampling period (Fig. 8). During subsequent periods Chl*a* was either relatively constant or declined slowly downstream. The downstream trends in Chl*a* in the Richelieu River water mass were highly variable with no consistent pattern either between sampling periods or as a function of transport time. In the Great Lakes water mass Chl*a* decreased quickly as the river water entered the lake but then increased as this water mass neared the outflow of the lake (see below).

In the Ottawa River water mass Chl*a* decreased rapidly when the river entered the lake on two sampling dates and then remained at between 2 and 4 $\mu g \cdot L^{-1}$. POC concentrations declined steadily downstream in all water masses with the exception of the Great Lakes water mass where the more typical U-shaped pattern was observed (Fig. 8).

Stepwise forward multiple regression analyses conducted on all data (all stations in water masses) revealed that most of the variation in Kd_{340} was due to *a*CDOM on all sampling dates (Fig. 9). However after June 8, the contribution of particulate material to light attenuation increased significantly until the end of the sampling season. On June 27 both Chl*a* and especially inorganic dry weight contributed to the explained variance. On July 18 Chl*a* and also absorbance due to particulate matter were important covariates whereas on August 18 inorganic dry weight contributed again contributed to the explained variance.

RDA analysis - UV radiation (UVR) and DOC are contributing the most to the separation of the four water masses during the whole sampling season (Fig. 10) as the effect of time has been removed (cruise used as a covariable). UVA and UVB penetration is decreasing with higher DOC concentration whereas PAR is decreasing with increasing amount of particles (Beam C attenuation). Light available for photosynthesis (PAR) doesn't change much between the four water masses. However, PAR and hence particles explain much of the variation within the Ottawa water masses and contribute, along with DOC, to the variation in the Great Lakes water mass. Stations located in the maritime channel show little variation amongst sites. UVR penetrates more deeply in the Great Lakes water mass which contains the lowest amount of DOC. Conversely, the Saint-François water mass contains the highest amount of DOC and UV penetrates least. Therefore, both DOC and particulate material are contributing to UV and PAR attenuation. The relationship between light attenuation and particulate matter increases with longer wavelengths whereas the relationship between light attenuation and DOC decreases with shorter wavelengths.

Discussion

Lake Saint-Pierre has recently been classified by UNESCO as an "ecological reserve of the biosphere" and is now officially recognized as a world heritage site. This recognition arose, in part, because of its high biodiversity; the lake supports 83 fish species and 288 bird species (Langlois et al. 1992). It is a very productive and unique ecosystem (Vincent and Dodson 1999) characterized by a variety of habitats including; extensive wetlands (6,900 ha), embayments, shallow and deep lotic sections that differ greatly in their residence times as well as numerous incoming tributaries with diverse physico-chemical characteristics.

Lake Saint-Pierre is the largest fluvial lake (~400 km^2) of the St.-Lawrence River ecosystem, one of the three largest rivers in North America. The St. Lawrence River, with a mean total annual discharge of 400 km^3, flows 1960 km from the Great Lakes until it reaches the margin of the continental shelf in the Atlantic Ocean. Patterns and processes in this lotic landscape are strongly influenced by the direction of downstream water movement (Ward, 1989; Townsend, 1996). Directionality is so pervasive in lotic ecosystems that system structure and ecological connectivity can be divided into longitudinal, lateral and vertical vectors with regard to the direction of flow (Ward, 1989; Ward and Stanford, 1995). We suggest that the high productivity and biodiversity of Lake Saint-Pierre can be explained by the combination of lentic characteristics found in shallow lakes coupled with the fundamental attributes of lotic systems; attributes such as directionality, heterogeneity and hierarchy which, taken together, enrich and multiply spatial and temporal linkages (connectivity) between habitats.

Shallow lakes: an extended littoral area - The littoral zone plays a major role in the functioning of lake ecosystems. It is the zone of highest productivity per unit area because of the high proportion of light available for photosynthesis and the transfer of carbon and nutrients from the adjacent terrestrial ecosystem (Wetzel, 2001). In deep lakes there is more light available in littoral than in pelagic zones on a 1% depth irradiance basis (Frenette and Vincent 2003). In contrast, fluvial Lake Saint-Pierre is a shallow-water ecosystem with adequate irradiance for photosynthesis and macrophyte development throughout the water column. This high irradiance contributes to greater plant productivity in littoral regions which, in turn, favors greater production of higher trophic levels. The major portion (area) of Lake Saint-Pierre, with the exception of the maritime channel, can thus be viewed, from the underwater light climate perspective, as an extended littoral zone.

From the nutrient perspective, the nearshore water masses can be viewed as ecotones receiving some of their water as drainage from adjoining wetlands (ref). These areas are therefore more directly coupled to terrestrial (allochthonous) inputs. Some of the inflowing tributaries (rivers) can also be viewed as injecting terrestrial inputs into the system. For example, the highest CDOM and DOC concentration were found in the nearshore waters of the Saint-François and Ottawa River derived water masses of Lake Saint Pierre (Figs. 2-5). These terrestrial inputs provide allochthonous CDOM as well as N and P released from agriculture activities in the respective watersheds of each tributary.

The maritime channel is the most prominent deep zone (average 12 m deep and ~245 m wide) in the lake. One feature distinguishing fluvial Lake Saint-Pierre from other shallow lakes is the large connectivity with upstream watershed processes. There are 14 different tributaries that flow into the lake. However, of these there are four main tributaries that make the greatest contribution to the horizontal stratification and spectral heterogeneity of Lake Saint-Pierre's waters (Frenette et al. 2003).

Here we show that fluvial Lake Saint-Pierre, as a representative of shallow lakes, is physically very heterogeneous and represents a mosaic of habitats physically connected to upstream processes of the main river network and tributaries at various spatial and temporal scales. The spatial heterogeneity or physical complexity will be described mainly in terms of bio-optical and chemical characteristics in relation to transport time derived from hydrodynamic simulations.

Spatio-temporal heterogeneity in habitat structure

Fluvial lake ecosystems: A mosaic of transport times (ages) - One distinguishing feature of fluvial lakes is the general reduction in water velocity as each water masses enters the shallow depths and wider areas (greater volume) of fluvial lakes. This results in an increase in, transport time of the various water masses within the lake. An important point is that such increases occur differentially for each water mass depending on basin morphology within the fluvial lake as well as discharge rates of each incoming tributary.

Although an intuitively obvious concept, actual measurements of spatial variability in ages of fluvial lake water masses are generally lacking in the literature.

Differences in transport times translate into differences in the time a particular water parcel spends in the lake before being swept back into the St. Lawrence River at the downstream end of the lake such that particles at different locations within a water body have different ages relative to the time they entered the lake (Monsen et al. 2002). The physico-chemical characteristics of the water masses are further modified by seasonally-shifting patterns in macrophyte density and species composition which are superimposed over the main downstream flow patterns (Morin et al. 2000). Our results also indicate that changes in water level strongly affect transport time dynamics within each water mass (connectivity on the vertical dimension). Our results clearly demonstrate the general deceleration of all water masses entering Lake Saint-Pierre especially for those water masses distributed in the nearshore areas of the lake i.e. Saint-François and Ottawa River water masses. This effect is much more pronounced in the southern portions of Lake Saint-Pierre; a region which also corresponds to the area of highest biological productivity.

Every lateral (North-South) transect across the lake is thus a mixture of water masses with different ages and origins (i.e. different tributaries) and temperatures. These differentially-aging water masses are influenced by within-lake processes further downstream.

A mosaic of underwater light habitats

Limnologists conducting primary production studies are always concerned with the vertical dimension; in part because of the requirement to precisely quantify the light climate available for photosynthesis in the water column. However, despite its importance, very few studies (but see; Smith et al. 1999; Frenette and Vincent 2003) have documented the horizontal variation in underwater light environment in lakes, fluvial lakes and rivers.

We measured characteristics of the underwater light spectra and select dissolved and particulate physico-chemical properties in the different water masses of Lake Saint-Pierre. We used these variables as tracers to reveal the extent and magnitude of spatial and temporal variability characteristic of this large and hydro-dynamically-complex fluvial lake. Our analysis of spectral components of the different water masses integrates the effects of seasonal changes in water levels, light-attenuating chemicals (e.g. CDOM) and suspended particles and highlights the large spectral heterogeneity in underwater conditions that may be encountered in fluvial lakes as well as the utility of bio-optical approaches in defining the magnitude of site-to-site variation in all dimensions.

North-South axis (transverse variability) - The greatest variability in optical measurements was due to differences in inherent properties (e.g. CDOM, inorganic and organic particles) amongst the water masses. Downstream morphological features such as; the presence of submerged macrophytes (Martin et al. in prep), wetlands draining into the lake along shorelines (e.g. embayments), variations in depth and, the extent of wind-induced suspension of light attenuating pigments further modified optical signatures. This variability was broadly expressed in terms of spatial and temporal patterns in PAR and UV attenuation.

Seasonal changes in water levels also influenced the distribution of water masses through the reduced contribution in area and volume of nearshore waters such as the Saint-François and the Ottawa River water masses (Fig. 1). This had the effect of increasing the dominance of Great Lakes waters later in summer. There was broad consistency, between 2000 (see Frenette et al. 2003) and 2001 (this study), in gross spatial and temporal patterns in spectral signatures amongst the main water masses indicating the temporally-stable uniqueness of the water masses. These unique characteristics, in effect, function to impose first-order selection pressures on biological communities.

Upstream-downstream axis (longitudinal variability) - The water masses of Lake Saint-Pierre are further modified during their downstream journey resulting in dynamic changes to their spectral signatures as a direct function of their transport time. For instance, water masses originating from the slow-moving nearshore St.-François and Ottawa River water masses show increased PAR and UV penetration downstream whereas optical characteristics of the fast-moving Great Lakes and Richelieu River water masses remain generally stable.

This bio-optical variability within nearshore waters can be explained, in part, by the longer transport time of these water masses which provides more time for UV- and microbial-degradative processes to operate. Because of the shallow depth, these UV exposed zones also occupy a large portion of the water column (see Figs. 2-5). Furthermore, UV photochemical (oxidative) reactions and microbial processes may increase UVR penetration in the water column because of bleaching of allochthonous CDOM (Osburn et al. 2001; Gibson et al. 2000) and bacterial production of autotrophic DOM by degradation of recalcitrant CDOM (Osburn et al. 2001; Wetzel et al. 1995). Time series exposures of Saint-François River water to natural UVR and microbial activity revealed a daily decrease in recalcitrant DOC (CDOM) concentration with concomitant production of labile carbon during a period corresponding to its observed transport time of 7-15 d within Lake Saint-Pierre (Trudel et al., in review). Such changes in inherent and emergent properties were not observed in the Great Lakes water mass. This can be explained by the, a) high transport times of this water mass in LSP, b) fact that the source water is relatively old (residence time of water in Lake Ontario is ~100 years) and, c) minimal lateral mixing with adjacent water masses. Thus, the Great Lakes water mass is one that has been affected by long-term exposure to UV and microbial processes long before it enters Lake Saint-Pierre. From this perspective the Great Lakes water mass may be considered an ancient expressway surrounded by modern service lanes.

Seasonal changes in spectral composition and UVR penetration - The penetration of UVR was strongly controlled by CDOM and, to a lesser extent, by the amount of seasonally increasing particulate matter concomitant with decreasing water levels. The importance of CDOM to UV attenuation is well-known (e.g. Scully and Lean; Arts et al. 2000a) but recent findings (Belzile et al. 2002; Vincent et al. 2001; Smith et al. 1999) demonstrate a significant contribution of particulate matter to UV attenuation in terms of absorption and scattering. Our results supports these findings but also demonstrate the dynamic nature of DOM and particulate matter to UVR attenuation with time as well as the interplay between absorption and scattering. To our knowledge, most studies which have addressed spectral attenuation in a restricted time frame do not consider the changing nature of the environment in relation to spectral attenuation. Our study demonstrates the influence of seasonal changes in water levels on light attenuation. The increasing contribution of particulate matter to UV attenuation may be related to decreasing water levels in the incoming tributaries later in the season which increases particle concentrations.

Macrophytes may behave as a sink or a source of particles in the water column and may therefore play a major role in controlling light heterogeneity. As a sink, they act as very efficient particle filterers which, in turn, contributes to higher UV penetration (Frenette and Vincent 2003). As a source, macrophytes release trapped particles (drifting inorganic and organic material) and associated periphyton during wind-induced mixing events which increases the concentration of particulate matter (Frenette, unpub. data). They may also slough off material towards the end of the growing season as they senesce contributing to CDOM pools in downstream portions of the lake.

Changes in lateral connectivity in temperate flood-plain systems remain poorly documented. There is an urgent need for more empirical data that addresses the dynamic nature of different riverine floodplains in terms of expansion and contraction cycles occurring well below bankfull ("flood pulse" versus "flow pulse") (Tockner et al. 2000). This study illustrates the short-term effects of flow pulse on inherent properties of the water (e.g. DOC, particulate matter) and its consequences for the underwater light environment. Such rapid change in habitat size, although generally neglected by stream ecologists, is a fundamental property of lotic systems. This is especially true for riverine floodplains that are by nature expanding and contracting. Each phase represents a change in connectivity of the water masses with wetlands which influence the magnitude of matter and energy transfers. These water level fluctuations, occurring well below bankfull, in Lake Saint-Pierre may considerably enhance floodplain productivity as observed in European river systems (Tockner et al. 2000).

Ecological implication of heterogeneity

Implications of spectral heterogeneity on productivity - The shallow portions, especially along the south shore, of Lake Saint-Pierre are very productive and support a large commercial fishery (Guénette et al. 1994). Perch (*Perca flavescens*) and American eel (*Anguilla rostrata*) growth rates are highest in the south water mass (Guénette et al., 1994 and Mailhot, 1998, respectively) as are densities (as revealed by catch-per-unit effort data from experimental gill net sets) of perch and other fish species (Fournier et al., 1998). Finally, commercial fisheries are preferentially located along the south shore (Langlois et al., 1992).

The greater average PAR irradiance in the water column contributes to higher plant productivity of the South water masses which, in turn, is likely to favor production at higher trophic levels. Light quality and quantity has been shown to influence the lipid (Arts and Rai, 1997, Wainman et al. 1999, Arts et al. 2000b) and stoichiometric composition (Sterner and Elser 2002) of primary producers. Sestonic Chl*a* and POC concentrations were highest in the south during the maximum expansion of the St. François River water mass in June. This corroborates a recent study in Lake Saint-Pierre which demonstrated higher biofilm (periphyton) biomass in the South compared to the North; a phenomenon which was attributed to higher light levels in the south (Huggins et al., in review, and see Figs. 2-5).

This gradient of transport time suggests that heat, plankton, benthic algae, macrophytes, and dissolved substances will accumulate preferentially in the nearshore areas and especially in the south. In support of this, temperature, phytoplankton biomass and CDOM show higher values in nearshore water masses (Figs. 2-5). Our results agree with Bukaveckas et al. (2002) who reported increased phytoplankton and bacterial biomass with water residence time in a large river impoundment. Similarly, in marine waters, Lucas et al. (1999) concluded that growth dynamics of a patch of phytoplankton in a tidal flow is a function of the total amount of time spent in a particular environment. Longer residence times are generally associated with more complex food webs, higher biodiversity and higher productivity. The classic empirical model of lake eutrophication (Vollenweider 1976) describes algal biomass as a function of phosphorous loading rate scaled by hydraulic residence time. Variable retention has been used to describe variability in dissolved organic carbon concentrations (Christensen et al. 1996) mineralization rates of organic matter (den Heyer and Kalf 1998) and primary production (Jassby et al. 1990). As emphasized by Reynolds et al. (1991), storage zones of rivers (e.g. slow-flowing side channels) are likely to be important sites for maintaining stocks and supporting growth of river phytoplankton but little is known about the St. Lawrence River in this regard.

UV penetration in nearshore water masses of Lake Saint-Pierre is also likely to promote positive effects on productivity by increasing photodegradation of otherwise refractory CDOM, thereby enhancing bacterial growth by providing lower molecular weight carbon substrates (Waiser and Robarts 2000, Wezel et al. 1995). Higher bioavailability favors higher carbon transfer to bacteria and, potentially, to higher trophic levels (Wetzel, 2001). The higher fish productivity observed in southern regions of Lake Saint-Pierre is likely explained by a combination of slow transport time, greater temperatures and light and superior bioavailability of carbon to higher trophic levels.

Implications of spatial heterogeneity on species diversity - These results draw attention to the large microhabitat variability on both horizontal (longitudinal and lateral) and vertical (water column depth) dimensions of Lake Saint-Pierre. The bio-optical variability amongst the water masses contributes to an increased physical complexity in Lake Saint-Pierre and other similar fluvial lake ecosystems, thereby favoring a broad range of species. Biodiversity in this lake is currently recognized only at upper trophic levels (i.e. birds and fish). However, M'Radamy et al. (unpubl.) demonstrated a higher phytoplankton and microzooplankton species number and higher densities in the South versus the North nearshore water masses relative to the Great Lakes water mass.

Optical conditions may operate as strong selective pressures for organisms living in a given area of the lake. For example, in terms of light intensity, phycobiliproteins in cyanobacteria absorb PAR over a much wider range of wavelengths allowing them to occupy low light environments (Oliver and Ganf 2000). Periodically changing light regimes, on the order of days (temporal heterogeneity), have been found to affect phytoplankton species composition and diversity (Flöder et al. 2002). Under permanent high light conditions chlorophytes dominated phytoplankton biomass while under permanent low light diatoms were the most abundant (Flöder et al. 2002).

In terms of light quality, greater UV exposure or other changes in spectral composition may involve the disappearance of sensitive species or selection for UV-resistant species (Xenopoulos and Frost 2003). Greater exposure in nearshore water masses may result in a higher potential for UV-induced damage of living organisms via a range of mechanisms (Vincent and Neale 2000). However this continuous high exposure in nearshore waters may also select for UV tolerant organisms, especially those that cannot escape from UV exposure by moving out of the bright irradiance regime (Roy 2000). Variability in light environments may thus influence shifts in biodiversity and succession as reported for phytoplankton (Litchman and Klausmeier 2001; Floder et al. 2002) and periphyton (Huggins et al, in review). In Lake Saint-Pierre, high spatial heterogeneity in physical, chemical and optical variables may act to increase opportunities for a more diverse array of organisms to successfully colonize the lake leading to more diversified communities. As discussed by Ward and Tockner (2001 and refs therein), this newer concept of biodiversity encompasses all levels of organization while integrating biotic and abiotic patterns and processes across different temporal and spatial scales.

Paradigms

Lakes and rivers and the vertical paradigm - In order to reduce physical complexity of aquatic ecosystems, lentic ecologists sometimes intentionally reduce their vision of space to 2 dimensions, for example, emphasizing the vertical axis, in order to explain the functioning of lake ecosystems. Traditionally, limnologists were mostly concerned with lakes that stratify in summer and where thermal stratification largely isolates the upper layers (epilimnion) from colder deep water (hypolimnion) and from interactions with sediments (Scheffer 1998, Wetzel 2001). Most changes in biological and physico-chemical variables were considered from the perspective of this vertical axis. For instance, seasonal patterns of mixing and stratification have been shown to control nutrient availability in the epilimnion; i.e. where material loss from the epilimnion is mineralized in the hypolimnion and can only return to the epilimnion after fall turnover. Other examples include primary production and light available for photosynthesis, vertical migration of zooplankton and their predators, geochemical exchanges, thermal habitat partitioning for fish etc. (e.g. see Kalff 2002 and/or Wetzel 2002). This vertical paradigm has been applied successfully to the study of deep or large waterbodies that stratify (e.g. Shield lakes, The Great Lakes etc.) but that also feature limited influence of macrophytes or wind-induced resuspension of sediments. Depth plays a fundamental role in relation to stratification, mixing regimes, and vertical forcing of such lake systems.

In contrast, shallow lakes are generally not stratified (polymictic). Their entire water column mixes frequently driven by wind action. This action promotes biological and chemical exchanges between sediments and the pelagic zone. As a result, nutrients are not systematically and unidirectionally lost from the pelagic zone because the intense sediment-water interaction ensures a rapid return of most recently sedimented material into the water column. Perhaps because of this, nutrient concentrations in shallow lakes tend to follow the opposite seasonal pattern of what is generally observed in stratified lakes (Jeppesen et al. 1997; Riley and Prepas 1985). Their shallow depth means that light, sufficient for photosynthesis (PAR), is generally available throughout the water column creating favorable conditions for macrophytes. This intense sediment-water contact and the potentially large impact of aquatic vegetation on sedimentation and resuspension makes the functioning of shallow lakes very different from that of their deep water counterparts in many respects (Scheffer, 1998).

Lotic ecologists have traditionally focused on the horizontal dimension; although more research is now being directed at incorporating the vertical effects of phreatic and hyphoreic inputs on ecosystem dynamics (Ward and Tockner 2001). At any one position in lotic systems patterns and processes occurring along each axis (longitudinal, lateral and vertical) may be remarkably different (Poole 2002). The main upstream-downstream patterns in the movement of materials contributes greatly to the high structural diversity of riverine landscapes at various scales; from the catchment scale to smaller scales of resolution such as between reaches or riffle-pool transitions. Because of the overriding effects of directional flow, longitudinal patterns in habitat variables along the course of rivers have served as a central theme in stream ecology.

Need for a new paradigm - The river continuum concept (Vannote et al., 1980) describes a continuum from a stream's headwaters to its mouth and is a reasonable representation of a general stream at the drainage basin scale. However, stream ecologists (refs in Poole 2002) now recognize that physical heterogeneity of various segments within a river actually represents a discontinuum rather than a continuum of stream segments (e.g. Townsend, 1996). Our results support a *discontinuum* view (Ward and Stanford 1983, 1995 and recently reviewed by Poole 2002) of lotic systems where river systems behave as adjacent river segments that differ markedly in connectivity.

These physical changes ultimately determine the pattern of variation in the extent of lateral and vertical connectivity along the river and ultimately the structure of biotic communities.

As indicated by Wiens (2002), "our failure to embrace spatial heterogeneity and fluvial dynamics as critical characteristics of lotic systems may be contributing to the lag in the rate of new idea generation". Bio-optical instrumentation (e.g. spectroradiometer, fluorometer) for direct underwater and remote sensing applications (i.e. satellite reconnaissance) offer us promising tools to study spatial variability and physical complexity at various vertical and horizontal scales. As shown here, in situ measurements such as spectral attenuation of UVR allow the rapid identification and characterization of water masses in lakes and rivers. Much more detailed measurements (e.g. fluorescence and/or absorption) can also be made to further explore relationships amongst physico-chemical and biological processes occurring within such lakes. Understanding factors which control light attenuation (e.g. CDOM and/or particulate matter) will provide further information on mechanisms responsible for controlling productivity and/or biodiversity of ecosystems.

Our results demonstrate the uniqueness of Lake Saint-Pierre in terms of spatial and temporal variability in optical and chemical properties as well as its overall connectivity with the St. Lawrence ecosystem. Lake Saint-Pierre is shallow, mostly unstratified and polymictic. The intense sediment-water interactions and presence of macrophytes further differentiates it from deep lakes. As a fluvial lake, Lake Saint-Pierre is also distinct from other shallow (non-fluvial) lakes because it is strongly influenced by upstream watershed processes and this imposes a strong directionality on the system. Inflowing tributaries inject subsidies with high amounts of nutrients, DOM and particulate matter into the lake. These subsidies add to the pool of local (*in situ*) C and nutrient released from wetlands. *In situ* transformation and resulting characteristics of dissolved and particulate matter will vary directly with transport time of each water mass. As a result the underwater light environment shows a strong horizontal stratification (gradient) on both the lateral and longitudinal axis. The strong spatial variability in light characteristics and the rich nutrient environment contributes to increase the physical complexity thereby favoring a broad range of species (biodiversity) and the high productivity characteristic of this lake.

Our study demonstrates that the vertical paradigm in lakes should now be extended to explicitly include the horizontal dimension so that we may gain a better understanding of spatial heterogeneity inherent in aquatic systems and its impact on living organisms. Future studies should address the relative impacts of longitudinal, lateral and vertical connectivity, at any given location and across a number of spatial scales, on community composition.

Modeling the description of the spatial heterogeneity is the next step for predicting linkages between physical and chemical processes and the biological components of aquatic ecosystems. Such processes are crucial to understanding the mechanisms that drive productivity and biodiversity in fluvial lakes and large rivers. This study illustrates the promise of applying optical variables, in conjunction with key physico-chemical variables, to construct 2D habitat models that, ultimately, will be used to predict biodiversity and productivity in fluvial lakes and large rivers.

Acknowledgements

This research was funded by, a) the Natural Sciences Research Council of Canada (NSERC) and the Fonds Québéquois de la Recherche sur la Nature et les Technologies (FQRNT-formerly FCAR) to J.-J. F., b) National Water Research Institute (NWRI), Environment Canada to M.T.A. and c) Meteorological Service of Canada to J.M. We thank Christine Barnard, Kim Huggins, Marianne Lefebvre, Pascal Lavallée, Marie-Audrey Livernoche, Sylvain Thélème and Geneviève Trudel for their invaluable help in the field and in the lab and the captain (Guy Morin) of the "Le Pêcheur" ship of the Meteorological Service of Canada, Environment Canada and captain Roger Gladu for sharing his experience and knowledge of Lake Saint-Pierre. This project is a contribution of the "Groupe de Recherche Interuniversitaire en Limnologie (GRIL)".

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Table 1. Discharge, volumes and surface areas of the four main water masses in Lake Saint-Pierre on the four sampling dates. Discharge values are given for stations located near the mouth of the respective tributaries. Other = Yamaska, Maskinongé and Du Loup water masses.

Water mass	Discharge ($m^3 \cdot s^{-1}$)	Volume (km^3)	% Total volume	Area (km^2)	% Total area
8-Jun-2001					
Great Lakes	7427.0	0.574	63.78	117.85	37.75
Ottawa	1369.0	0.166	18.40	64.65	20.71
Richelieu	547.8	0.062	6.84	24.51	7.85
St-François	331.8	0.078	8.64	76.18	24.40
Other	60.0	0.021	2.33	28.98	9.28
Total		**0.900**	**100.00**	**312.17**	**100.00**
27-Jun-2001					
Great Lakes	6753.0	0.519	69.39	119.73	41.82
Ottawa	903.6	0.126	16.89	57.45	20.07
Richelieu	408.1	0.057	7.59	29.37	10.26
St-François	62.0	0.032	4.33	47.46	16.58
Other	44.7	0.014	1.81	32.29	11.28
Total		**0.747**	**100.00**	**286.30**	**100.00**
18-Jul-2001					
Great Lakes	6746.0	0.523	70.92	118.45	43.14
Ottawa	780.7	0.107	14.46	54.40	19.81
Richelieu	282.9	0.038	5.15	16.96	6.18
St-François	147.0	0.052	7.07	62.66	22.82
Other	67.9	0.018	2.40	22.09	8.05
Total		**0.737**	**100.00**	**274.56**	**100.00**
13-Aug-2001					
Great Lakes	6630.0	0.488	79.22	131.99	50.79
Ottawa	509.7	0.076	12.39	47.15	18.14
Richelieu	158.7	0.036	5.90	29.71	11.43
St-François	18.9	0.009	1.52	26.43	10.17
Other	13.6	0.006	0.97	24.61	9.47
Total		**0.616**	**100.00**	**259.89**	**100.00**

Table 2. Station number assignments with respect to time and water mass distribution in Lake Saint-Pierre (see Fig. 1).

	Transect within Lake Saint-Pierre		
Water mass	**Upstream**	**Middle**	**Downstream**
6-Jun-01			
Saint-François	0,1,2,3	16,17,18	19,20,21,22
Richelieu	4	15	22x
Great Lakes	5,6	13,14	23,24
Ottawa	7,8	11	25,26
27-Jun-01			
Saint-François	1	18	19,20
Richelieu	2	14,15,16	22
Great Lakes	3,4,5,6	12,13	23,24
Ottawa	7,8,9	11	25,26
18-Jul-01			
Saint-François	1	15,16,17,18	19,20,21,22
Richelieu	too dilute	too dilute	22x
Great Lakes	4,5,6	12,13	23,24
Ottawa	7,8	11	25,26
13-Aug-01			
Saint-François	too shallow	too shallow	20
Richelieu	1	15,16	22
Great Lakes	2,3,4,5,6	12,13,14	23,24
Ottawa	7,8,9	10,11	25,26

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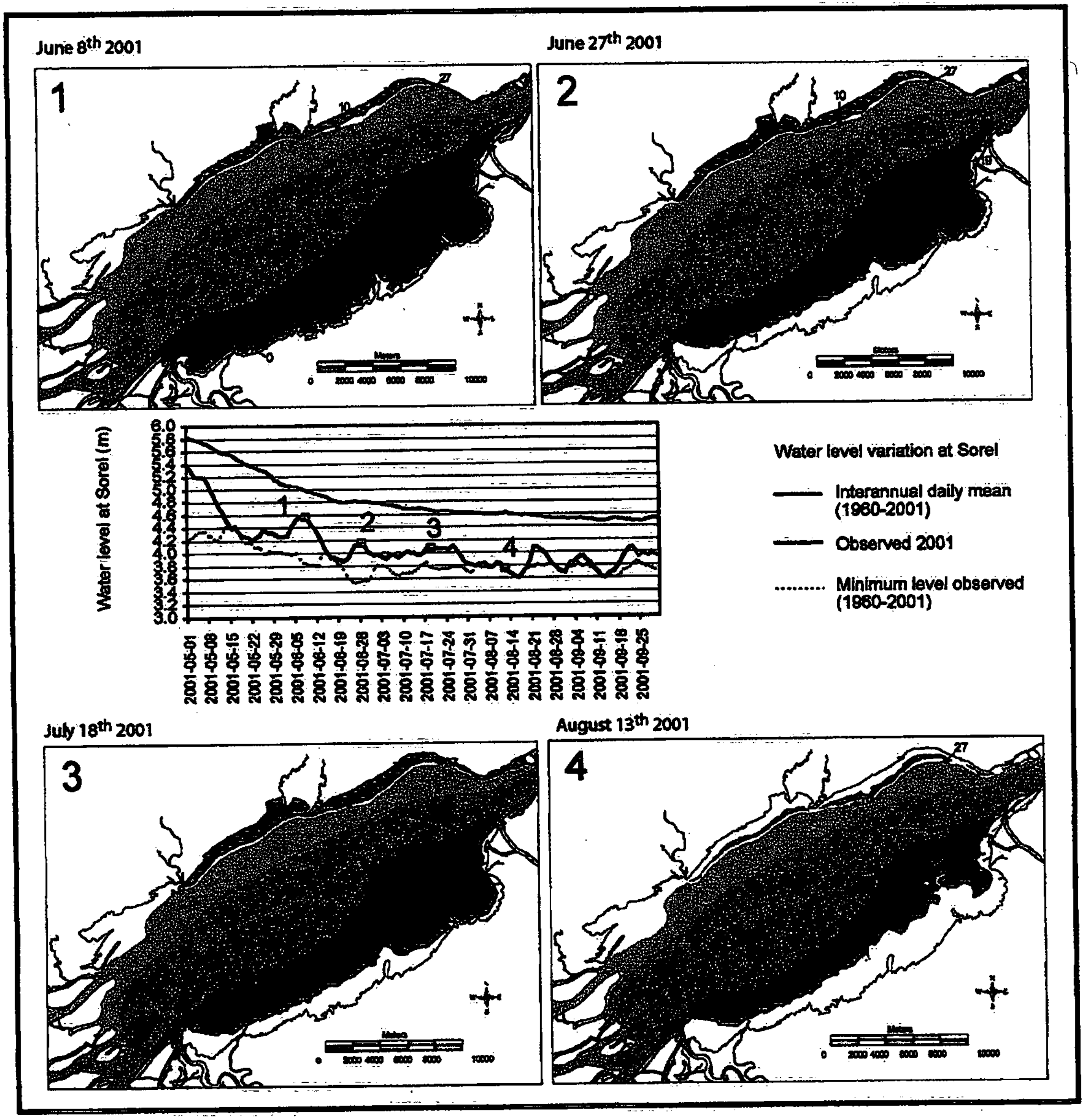
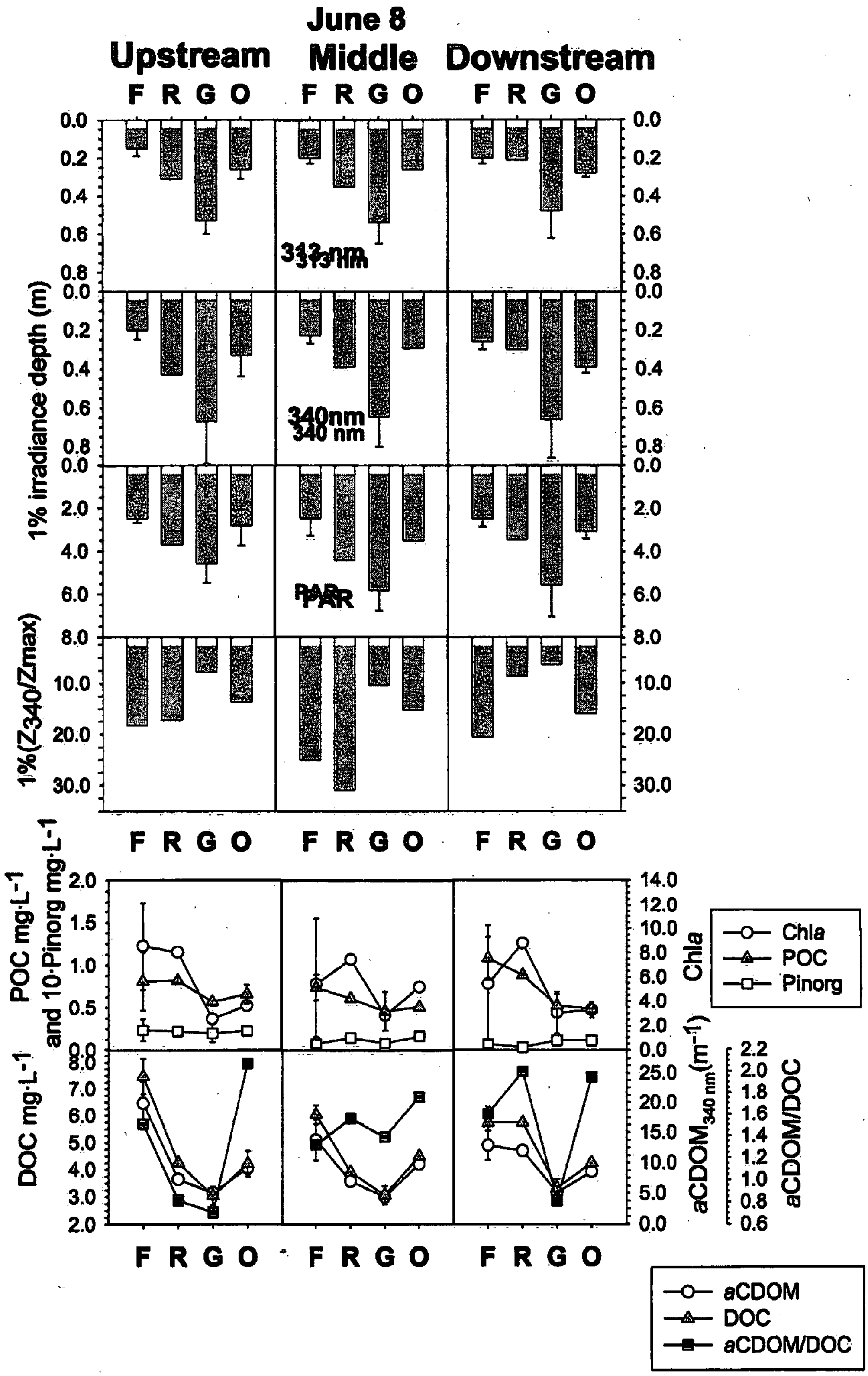
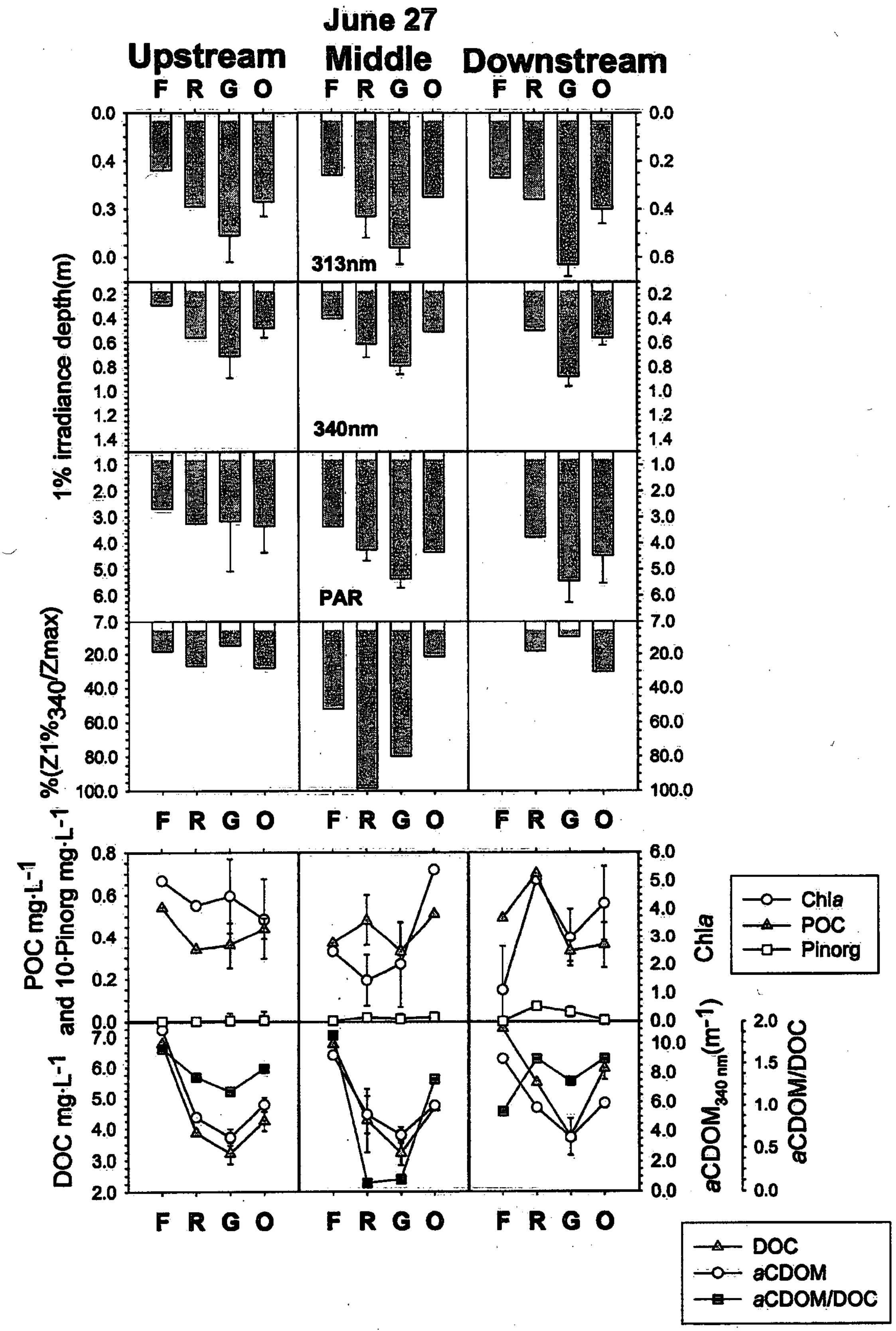
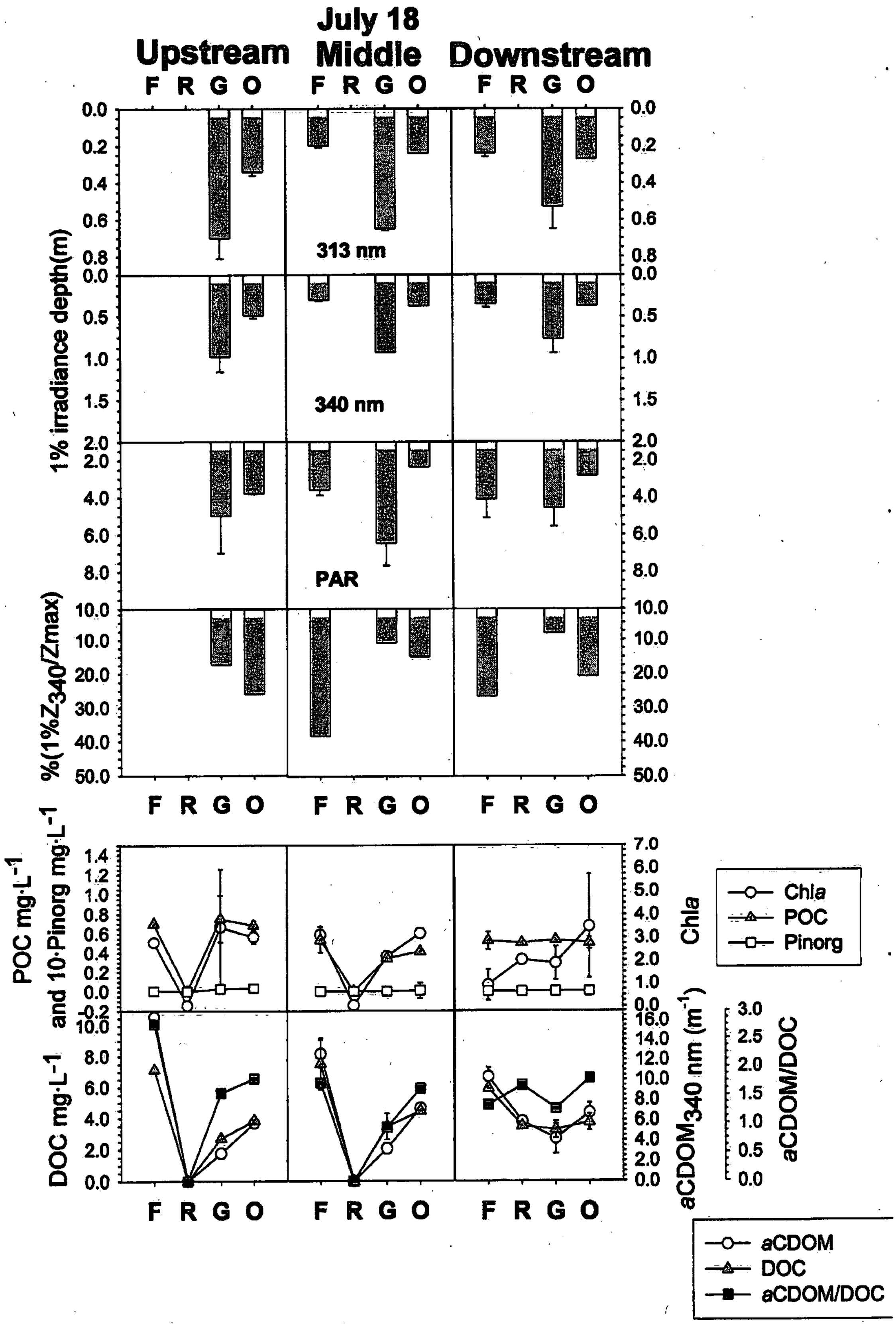
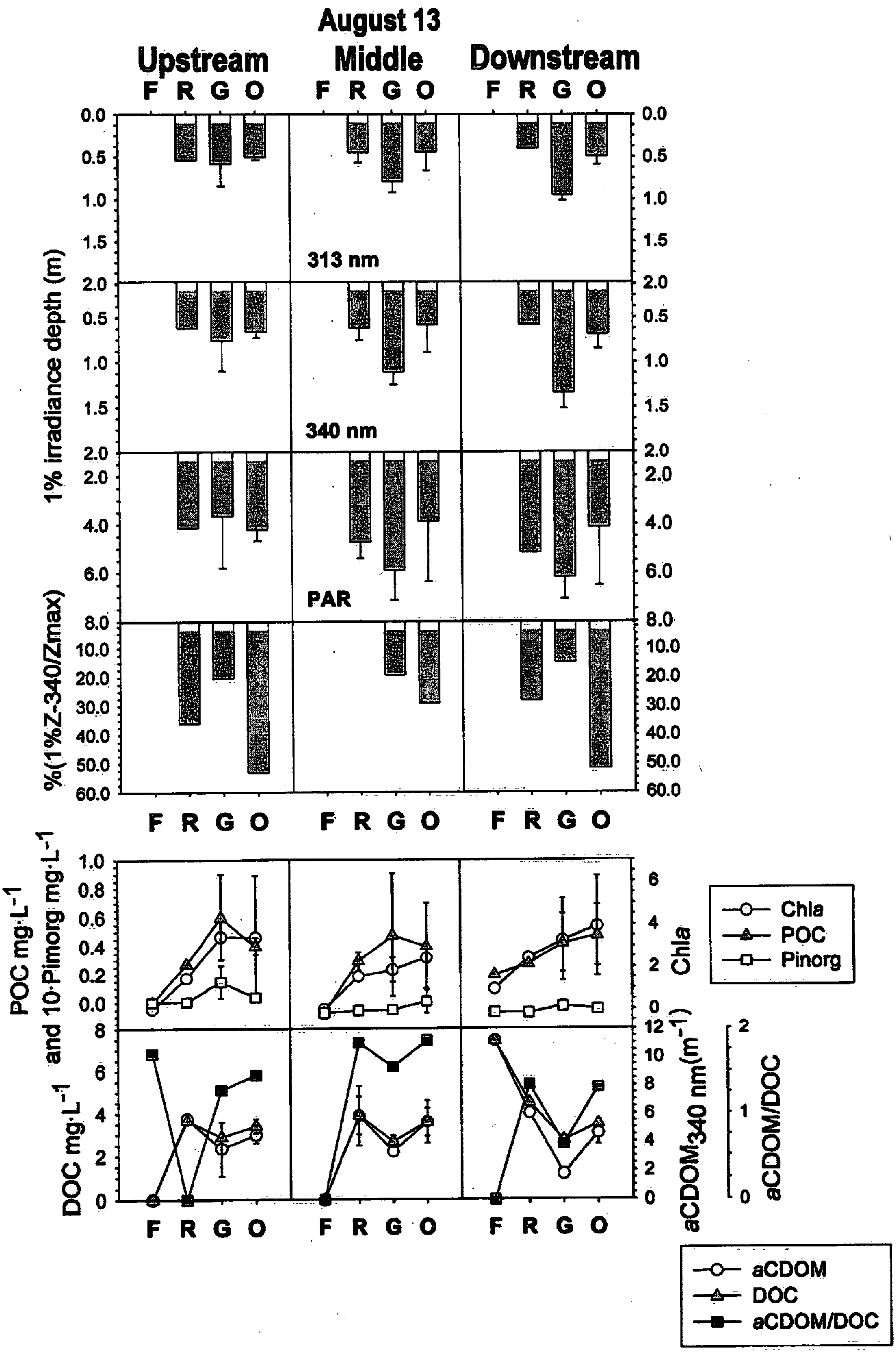
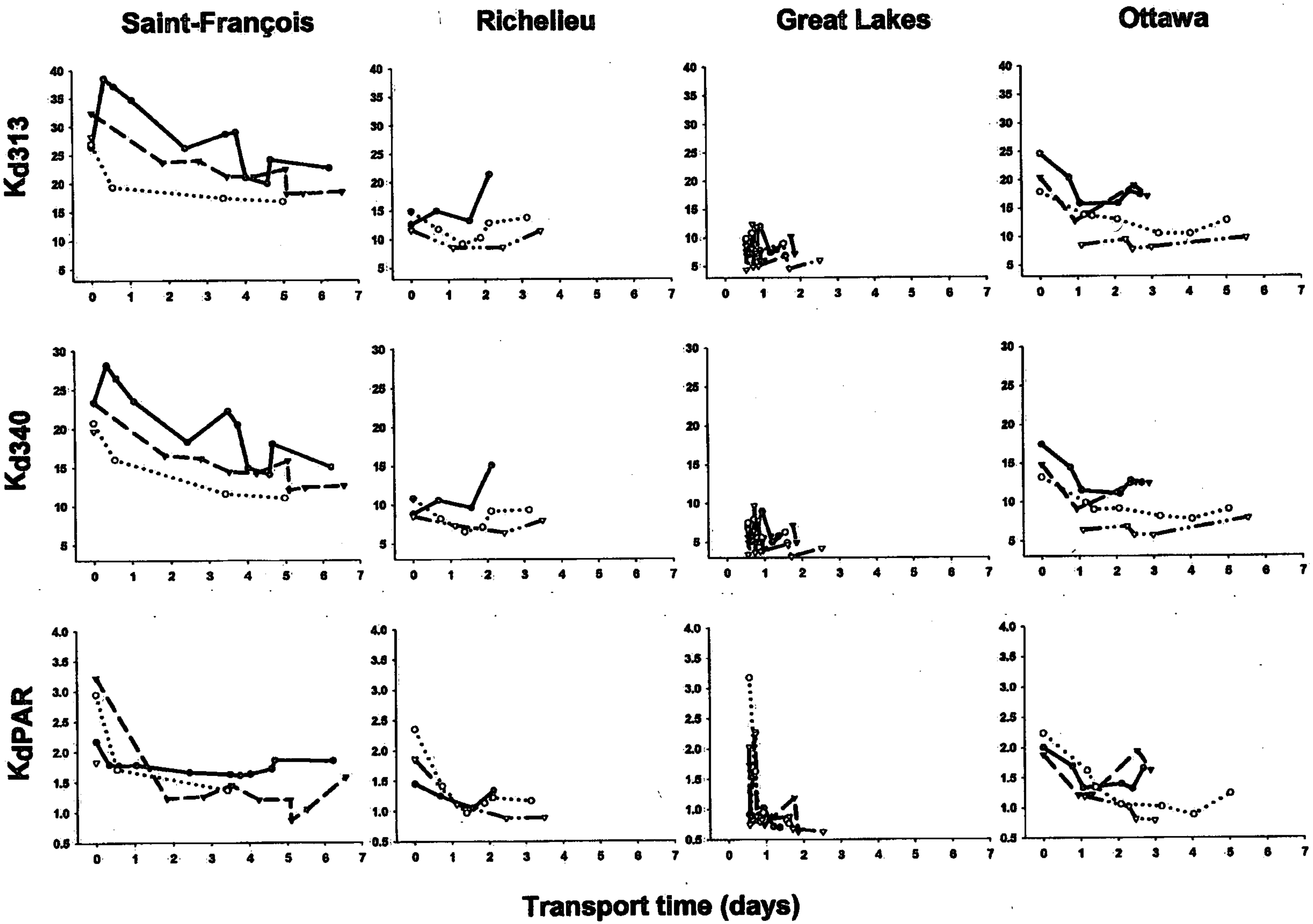

June 8th 2001
1
June 27th 2001
2
Water level at Sorel (m)
6.0
5.8
5.6
5.4
5.2
5.0
4.8
4.6
4.4
4.2
4.0
3.8
3.6
3.4
3.2
3.0
2001-05-01
2001-05-08
2001-05-15
2001-05-22
2001-05-29
2001-06-05
2001-06-12
2001-06-19
2001-06-26
2001-07-03
2001-07-10
2001-07-17
2001-07-24
2001-07-31
2001-08-07
2001-08-14
2001-08-21
2001-08-28
2001-09-04
2001-09-11
2001-09-18
2001-09-25
1
2
3
4
Water level variation at Sorel
Interannual daily mean (1960-2001)
Observed 2001
Minimum level observed (1960-2001)
July 18th 2001
3
August 13th 2001
4
Meters
0 2000 4000 6000 8000 10000
10
27

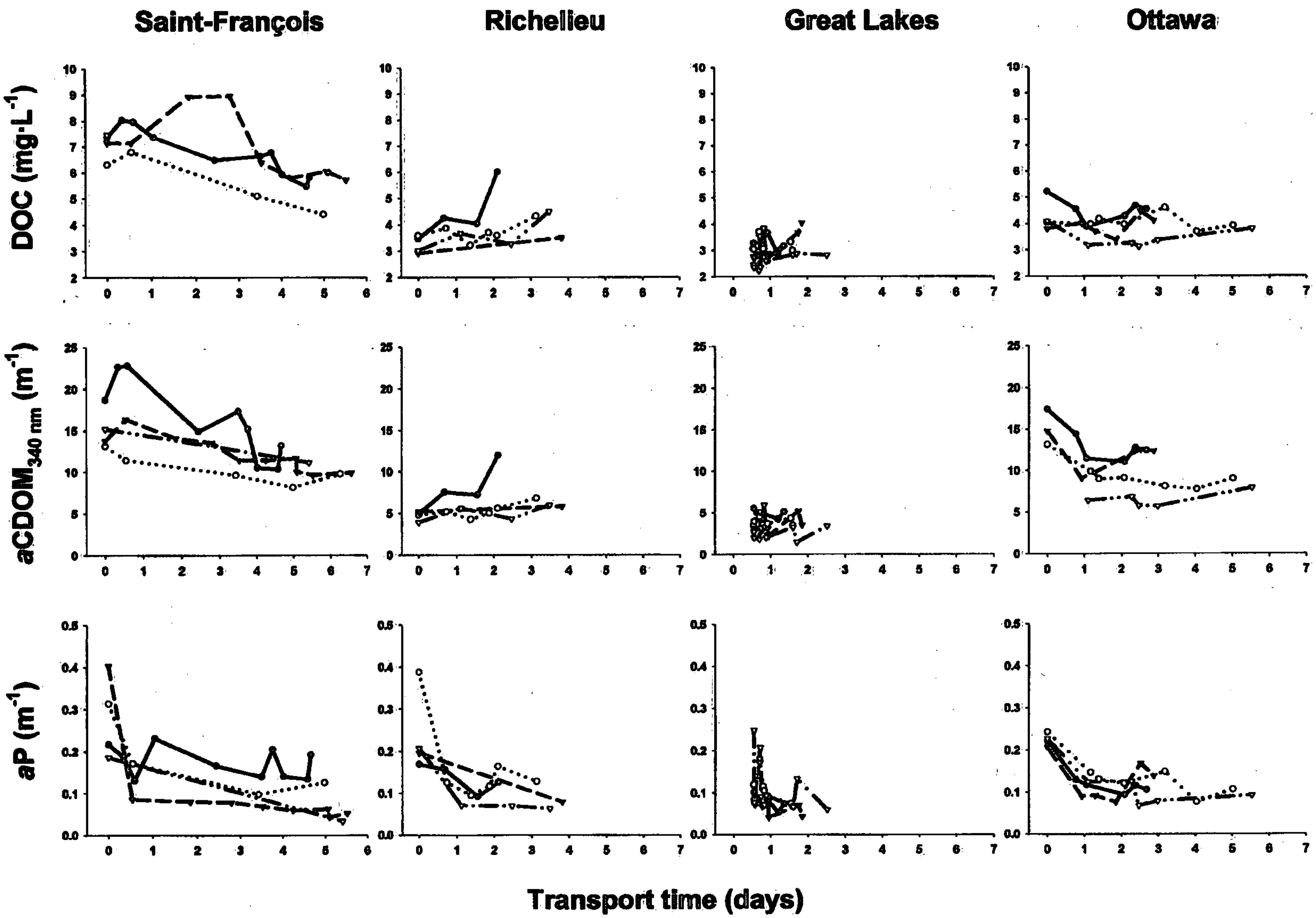

June 8
Upstream
Middle
Downstream
F R G O
F R G O
F R G O
0.0
0.2
0.4
0.6
0.8
313 nm
340 nm
PAR
2.0
4.0
6.0
8.0
10.0
20.0
30.0
1% irradiance depth (m)
1%(Z340/Zmax)
POC mg·L-1
and 10·Pinorg mg·L-1
0.5
1.0
1.5
2.0
14.0
12.0
10.0
8.0
6.0
4.0
2.0
Chla
Chla
POC
Pinorg
DOC mg·L-1
3.0
4.0
5.0
6.0
7.0
8.0
5.0
10.0
15.0
20.0
25.0
aCDOM340 nm(m-1)
0.6
0.8
1.0
1.2
1.4
1.6
1.8
2.0
2.2
aCDOM/DOC
aCDOM
DOC
aCDOM/DOC

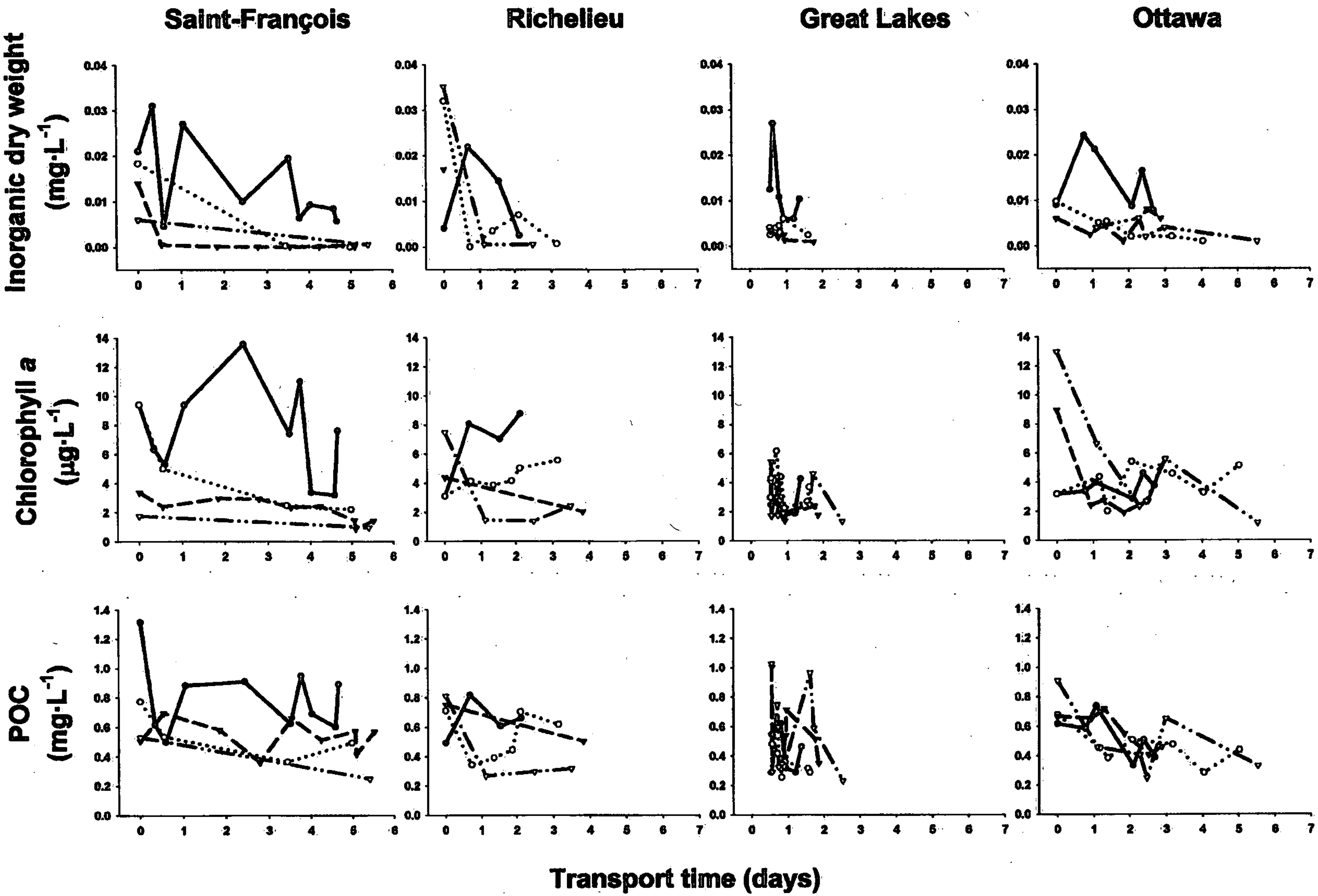

June 27
Upstream
Middle
Downstream
F R G O
F R G O
F R G O
1% irradiance depth(m)
313nm
340nm
PAR
%(Z1%340/Zmax)
0.0
0.4
0.3
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
2.0
3.0
4.0
5.0
6.0
7.0
20.0
40.0
60.0
80.0
100.0
POC mg·L-1 and 10·Pinorg mg·L-1
0.8
0.6
0.4
0.2
0.0
Chla
6.0
5.0
4.0
3.0
2.0
1.0
0.0
Chla
POC
Pinorg
DOC mg·L-1
7.0
6.0
5.0
4.0
3.0
2.0
aCDOM340 nm(m-1)
10.0
8.0
6.0
4.0
2.0
0.0
aCDOM/DOC
2.0
1.5
1.0
0.5
0.0
DOC
aCDOM
aCDOM/DOC

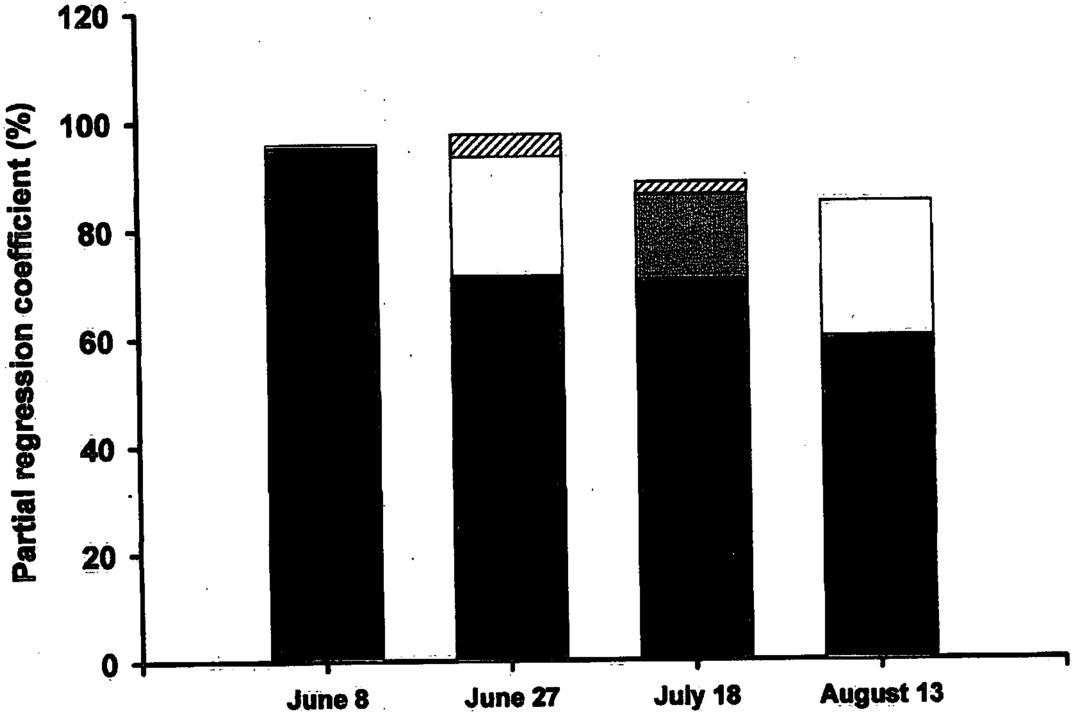

July 18
Upstream
Middle
Downstream
F R G O
F R G O
F R G O
1% irradiance depth(m)
313 nm
340 nm
PAR
0.0
0.2
0.4
0.6
0.8
0.5
1.0
1.5
2.0
4.0
6.0
8.0
10.0
%(1%Z340/Zmax)
20.0
30.0
40.0
50.0
POC mg·L-1 and 10·Pinorg mg·L-1
1.4
1.2
-0.2
7.0
5.0
3.0
Chla
Chla
POC
Pinorg
DOC mg·L-1
16.0
14.0
12.0
aCDOM340 nm (m-1)
2.5
aCDOM/DOC
aCDOM
DOC
aCDOM/DOC

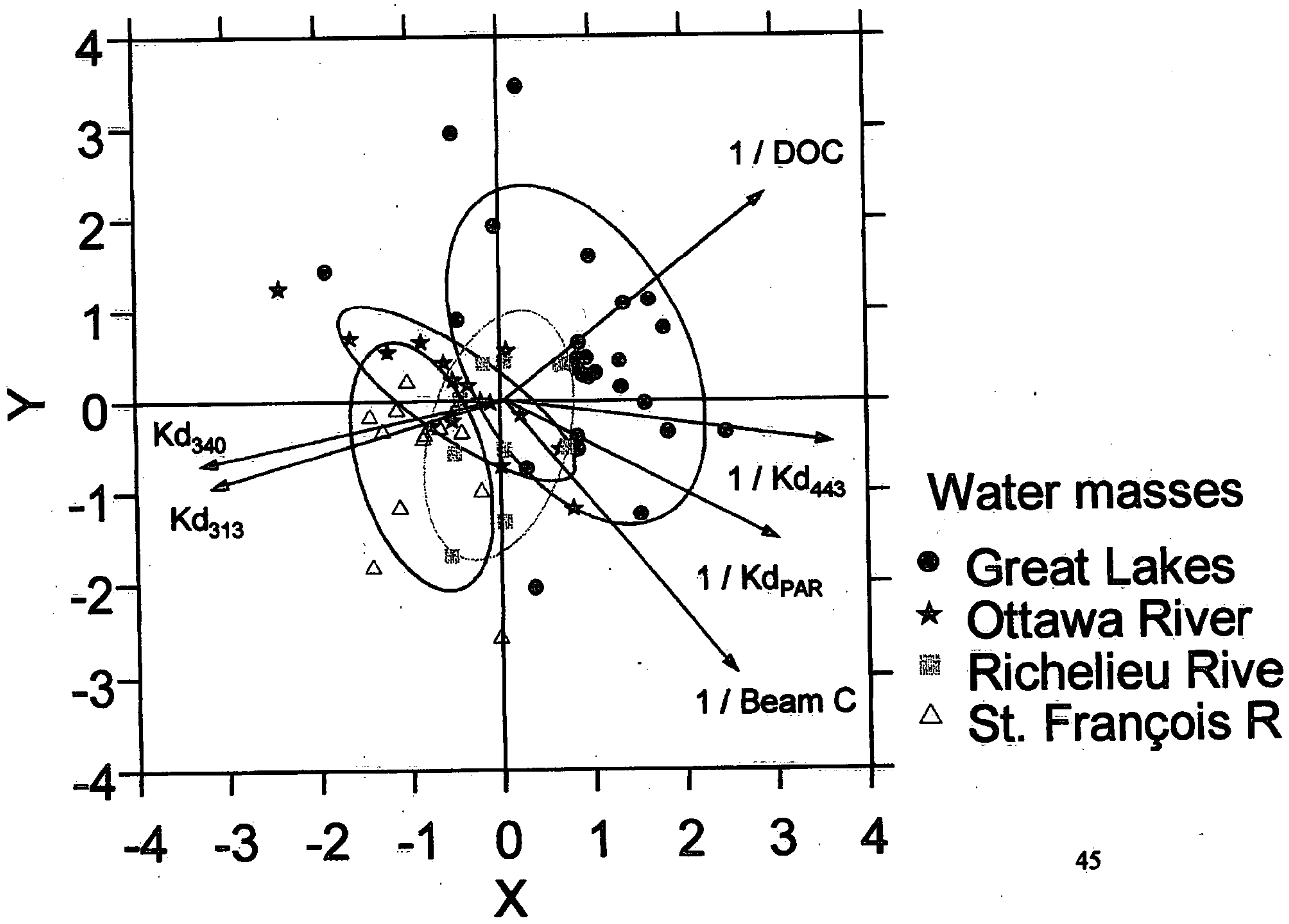

August 13
Upstream
Middle
Downstream
F R G O
313 nm
340 nm
PAR
1% irradiance depth (m)
%(1%Z-340/Zmax)
0.0
0.5
1.0
1.5
2.0
4.0
6.0
8.0
10.0
20.0
30.0
40.0
50.0
60.0
POC mg·L-1 and 10·Pimorg mg·L-1
Chla
Chla
POC
Pinorg
DOC mg·L-1
aCDOM340 nm(m-1)
aCDOM/DOC
aCDOM
DOC
aCDOM/DOC


Saint-François
Richelieu
Great Lakes
Ottawa
Kd313
Kd340
KdPAR
40
35
30
25
20
15
10
5
30
25
20
15
10
5
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0
1
2
3
4
5
6
7
Transport time (days)


Saint-François
Richelieu
Great Lakes
Ottawa
DOC (mg·L-1)
aCDOM340 nm (m-1)
aP (m-1)
10
9
8
7
6
5
4
3
2
25
20
15
10
5
0
0.5
0.4
0.3
0.2
0.1
0.0
0
1
2
3
4
5
6
7
Transport time (days)


Saint-François
Richelieu
Great Lakes
Ottawa
Inorganic dry weight
$(mg \cdot L^{-1})$
0.00
0.01
0.02
0.03
0.04
Chlorophyll a
$(\mu g \cdot L^{-1})$
0
2
4
6
8
10
12
14
POC
$(mg \cdot L^{-1})$
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
0
1
2
3
4
5
6
7
Transport time (days)


Partial regression coefficient (%)
120
100
80
60
40
20
0
June 8
June 27
July 18
August 13


Y
4
3
2
1
0
-1
-2
-3
-4
X
-4
-3
-2
-1
0
1
2
3
4
1 / DOC
Kd_{340}
Kd_{313}
$1 / Kd_{443}$
$1 / Kd_{PAR}$
1 / Beam C
Water masses
● Great Lakes
★ Ottawa River
▨ Richelieu Rive
△ St. François R

Environment Canada Environnement Canada

Canada

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