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Research Article

Effects of macrophytes and terrestrial inputs on fluorescent dissolved organic matter in a large river system

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Abstract. We studied the contribution of aquatic macrophytes and allochthonous sources to the pool of fluorescent dissolved organic matter (FDOM) in a large river system composed of several distinct water masses that flow alongside one another in the same riverbed. Using three dimensional fluorescence combined with parallel factor analysis (PARAFAC), we characterized FDOM found in the St. Lawrence River (Lake Saint-Pierre, Québec, Canada), and from macrophyte leaching experiments. Eight fluorescent components were identified, three of which were dominant in macrophyte experiments and were similar to protein-like, autochthonous fluorophores identified in previous studies. The remaining components corresponded to humic and fulvic acids, and a principal component analysis revealed that their distribution in Lake Saint-Pierre was different than that of protein-like fluorophores, suggesting a different origin. Concentrations of dissolved organic carbon were strongly associated with the distribution of the allochthonous components. The distribution of protein-like FDOM in Lake Saint-Pierre matched that of macrophytes in the lake and the abundance of allochthonous FDOM was explained by the connectivity with the terrestrial ecosystem. Nearshore water masses carrying large loads of newly imported organic matter from proximal tributaries showed the maximum abundances and the older water masses, from the center of the lake, carried smaller quantities of terrestrial organic matter, thus originated mainly from Lake Ontario, several hundred kilometers upstream of Lake Saint-Pierre. This study demonstrates that macrophytes are a net source of protein-like FDOM and could represent an important supply of autochthonous DOM in shallow, productive environments.

Key words. FDOM; macrophytes; fluvial lake; allochthonous; PARAFAC; river.

Introduction

Riverine ecosystems are fueled by organic carbon originating from numerous sources, including in-stream primary producers and the terrestrial landscape. In shallow aquatic ecosystems, light penetrates most of the water column, causing favorable growth conditions for macrophytes as well as suspended and

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attached algae. In addition to passing organic carbon to consumers, primary producers contribute, through excretion and decomposition, to the pool of autochthonous dissolved organic matter (DOM). Considering the relatively high bioavailability of this DOM, it can also contribute to overall lake and river metabolism by sustaining bacterial activity (Chen and Wangersky, 1996; Kritzberg et al., 2004). Sobek et al. (2007) demonstrated that concentrations of dissolved organic carbon (DOC) in lakes are influenced primarily by climatic and topographic characteristics and secondarily by catchment and lake properties. This suggests that factors external to the aquatic environment drive the allochthonous loadings of DOM and instream features dictate the transformation of this terrestrial organic matter and the cycling of autochthonous DOM.

In marine environments, where phytoplankton is the dominant source of organic matter, sources and forms of fluorescent dissolved organic matter (FDOM) have long been studied, using fluorescence analyses as a proxy of DOM (Ferrari and Mingazzini, 1995; Coble, 1996; Sondergaard et al., 2003; Stedmon and Markager, 2005a; among others). In fresh waters, high productivity and the proximity of aquatic to terrestrial ecosystems increase the complexity of the FDOM pool. Recent work has focused on the allochthonous FDOM originating from wetlands and terrestrial ecosystems (Hood et al., 2005; Mladenov et al., 2007) and on the autochthonous FDOM derived from microbial and phytoplankton sources (McKnight et al., 2001; Cory and McKnight, 2005; Hood et al., 2005). Macrophytes provide an important source of DOM in several environments (Martin et al., 2005; Fischer et al., 2006; Maie et al., 2006), yet little is known about the fluorescence properties of this DOM, especially in temperate aquatic ecosystems. Considering their abundant biomass in shallow, productive environments, macrophytes are likely to contribute significantly to the pool of FDOM that fuels the microbial loop. This study uses recent statistical developments in fluorescence analyses to characterize the FDOM originating from macrophytes and the terrestrial ecosystem in a large river system strongly influenced by wetlands, floodplain and tributaries.

Lake Saint-Pierre (lat 46°12' N, long 72°50' W), Québec, Canada, is the largest (400 km^2 with a mean discharge of approximately 10,000 m^3s^{-1}) fluvial lake of the St. Lawrence River. Its bottom is extensively covered by large beds of macrophytes that, together with their attached epiphytes, represent the most important primary producers in the system (Vis et al., 2007). The macrophyte distribution roughly follows the depth profile of the lake, with maximum abundances in the shallow littoral zone, decreasing toward the center of the lake. The beds reach their maximum biomass around mid-August then enter a senescent state around October, when temperatures and photoperiod decrease. The transition of macrophytes from growth to senescence is thus likely to seasonally influence the autochthonous FDOM pool composition.

Lake Saint-Pierre is also strongly connected with the terrestrial ecosystem through its extensive floodplain (180 km^2) and the confluence of seven tributaries with catchment areas that range from 269 km^2 to 23,720 km^2 (mean = 6,430 km^2). These contribute to the formation of up to eight distinct water masses in the river that flow parallel to one another, with the water mass in the nearshore zone composed of water imported from the nearest upstream tributary (see Frenette et al., 2006 for a figure illustrating the distribution of Lake Saint-Pierre water masses). The central water mass carries mainly the water flowing from Lake Ontario, situated 250 kilometers upstream of Lake Saint-Pierre. Because of contrasting land use in their respective catchments, and varying residence time and average water column depth, the water masses differ in their light spectral characteristics, nutrient concentrations, dissolved and particulate organic matter, and inorganic suspended matter (Frenette et al., 2006), resulting in a strong lateral heterogeneity. The composition of the FDOM pool is thus likely to vary tremendously on a lateral gradient as well as throughout the year due to seasonal changes in the macrophyte life cycle and the hydrodynamic regime.

Methods

Sampling

Three sampling surveys were performed during 2004, timed to approximately correspond with the different stages of the macrophyte life cycle: maximum abundance (August 18), senescence (October 7), and submerged drifting (November 4). Twenty-seven sites, distributed along three lateral transects comprising nine sites each, were sampled on each occasion (Fig. 1) in order to capture the variability in the FDOM pool caused by the different water masses and the various groups of macrophytes. Two litres of integrated depth water samples from the first 1.5 m of the water column were collected at each site using a 2-m long, 7-cm diameter polyethylene tube.

DOC and FDOM

From each site, 200 mL of water was filtered through a 45-mm diameter, 0.2-μm nominal pore-size polycar-

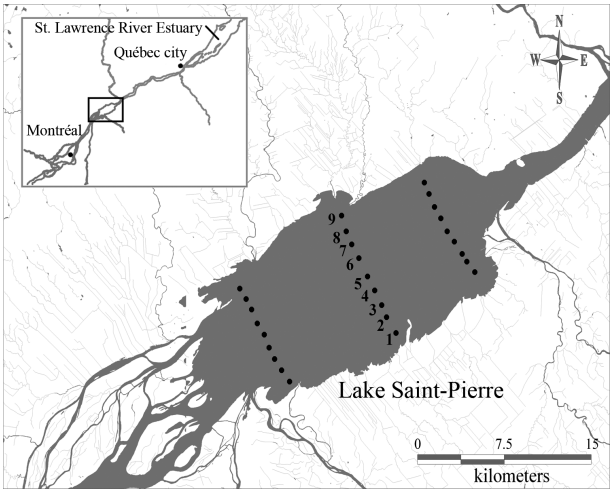

Figure 1. Distribution of sampling sites along three south–north lateral transects, position 1 being the southernmost site.

bonate membrane (Isopore, Millipore). Membranes were prerinsed with 100 mL of MilliQ water to remove potential impurities. Filtrate was stored in acid-washed borosilicate bottles and kept in the dark at 4 °C until analysis for FDOM fluorescence and DOC concentration. DOC concentrations were determined with a total organic carbon analyser (OI Analytical, TOC-1010) by sodium persulfate digestion. Absorbance and fluorescence scans were performed within two days after sample collection.

Macrophyte excretion experiment

Growing specimens of three species of macrophytes in Lake Saint-Pierre were collected during early summer 2006 to measure the fluorescence signature of FDOM leached during induced senescence conditions. *Potamogeton richardsonii* represented submerged species, being the most abundant representative of that group within the lake (Saint-Cyr and Campbell, 1990; Fortin et al., 1993). Emergent macrophytes included *Sagittaria latifolia* and *Scirpus sp.*, which are widely distributed within this group (Hudon, 1997). Plants were gently rinsed with distilled water in the laboratory, without removing their attached epiphytes. Specimens were allowed to decay separately in the dark for eight days in separate 2-L polyethylene bottles filled with distilled water. FDOM samples were collected from the decaying specimens on days 1, 2, 4 and 8. No DOC sample was collected, and no bactericide was added, in order to measure all possible forms of FDOM directly or indirectly originating from macrophytes under conditions similar to natural ones.

Optical analyses

Spectral absorption by the FDOM was measured on a dual-beam spectrophotometer (Shimadzu UV-2401 PC) with 1-cm quartz cells in the 190 to 900-nm range. The absorption coefficient **α** at 375nm was calculated according to the following equation:

$$\alpha_{\mathrm{CDOM}(375nm)} = \frac{2.303A(375nm)}{l}$$

where A is the absorbance and l is the path length in meters (Kowalczuk et al., 2006).

Three-dimensional excitation-emission matrixes were measured (230 to 600-nm emission wavelengths, 2-nm increments; 230 to 450-nm excitation wavelengths, 5-nm increments, bandwidth = 5 nm for both) on a Varian (Eclipse) fluorometer. The signal-to-noise ratio was very good in this range but deteriorated rapidly below 230 nm. Scans were corrected for inner-filter effect (McKnight et al., 2001) and standardized in Raman units (R.U.) (Stedmon et al., 2003). They were then corrected for instrument biases using an excitation correction spectrum derived from a concentrated solution of rhodamine B and an emission correction spectrum obtained using a ground quartz diffuser, as recommended by the manufacturer. Raman and Rayleigh scattering were removed from the EEMs prior to analysis by replacing these regions by a diagonal of NaN (not a number). The PLS toolbox (3.5) in Matlab 7.0 was used to perform PARAFAC analysis on 254 excitation-emission matrixes (EEMs), which included the samples from Lake Saint-Pierre and from the macrophyte excretion experiment, to identify the fluorescence components of the FDOM. The data set also included several samples from other lakes, but these were not analyzed in this study. These fluorescence components were subsequently validated by a split-half analysis (Stedmon et al. ,2003), and residuals were examined to ensure that no systematic variation was present. The parameters obtained from the PARAFAC model were used to calculate an approximation of the abundance of each component, expressed as $F_{\max}$ (in R.U.), which corresponds to the maximum fluorescence intensity for a particular sample.

Statistical analyses

A principal component analysis using a correlation matrix was performed on Systat (version 11, SSI, San Jose, U.S.) to explore the relationships between fluorescence components, optical parameters, and DOC concentrations for samples collected in Lake Saint-Pierre. Samples from excretion experiments were not included in this analysis. Data were normalized prior to analysis. Factors explaining more than 10 % of the variance were used.

Table 1. Characterisation of fluorescence components identified in this study and their correspondance with previously identified components (non-exhaustive list). Secondary maxima in brackets. References: (1) Stedmon and Markager, 2005a; (2) Stedmon and Markager, 2005b; (3) Cory and McKnight, 2005; (4) Ohno and Bro, 2006; (5) Fellman et al., 2008

Component	Excitation maxima (nm)	Emission maxima (nm)	Previously identified components Reference #				
			1	2	3	4	5
1	<230	452	C1		C2	C2	C1
2	265	446, 464	C1				
3	<230, 265	302	C8	C4	C13	C5	C9
4	<230 (280)	306, 476	C8	C1, C4			C9
5	250 (300)	374			C3		
6	390 (275)	482	C2	C7		C1	
7	340 (240)	422	C5		C9	C3	C4
8	<230 (280)	338	C7	C4, C6	C3	C4	C8

Results

Characterisation of fluorescence components

The PARAFAC model validated eight fluorescence components (Fig. 2). All components have been identified in previous studies (Table 1). Humic components 1 and 7 and protein-like components 3 and 8 appear to be present in a number of systems, unlike the remaining components (Table 1). All components showed multiple excitation peaks for one emission peak, except for component 4, with two emission peaks, and component 1, with one excitation peak. Protein-like components 3, 4, and 8 differed from the other five components in that they exhibited fluorescence in the lower wavelengths for both excitation (typically < 300 nm) and emission (typically < 400 nm) and were found in greater relative abundances in the macrophyte leaching experiments than in the natural lake water (Fig. 3). Component 4 was particularly dominant in the submerged macrophyte leaching experiment (Fig. 3).

Component 1, a group of fluorophores that dominates several aquatic ecosystems (Table 1), was approximately 2.5 and 8 times more abundant in FDOM from natural water than that leached from emergent and submerged macrophytes, respectively (Fig. 3) and represented the most abundant FDOM group in Lake Saint-Pierre. Considering that it represented almost 5% and 15%, respectively, of the total FDOM pool leached from submerged and emergent macrophytes, and was found in higher proportions in natural water, it probably originates from both autochthonous and allochthonous sources. It was associated with terrestrial sources of FDOM in previous studies (Stedmon and Markager, 2005a, and references therein). Components 2, 5, 6, and 7 corresponded to previously identified humic and fulvic acids of terrestrial origin. Moreover, their low abundance during the macrophyte leaching experiments demonstrated the poor contribution of macrophytes to the abundance of these components in natural water.

FDOM in Lake Saint-Pierre

The distribution of FDOM components in Lake Saint-Pierre illustrates their contrasting origins, as can be seen with the principal component analysis (Fig. 4), in which the first two factors explain 83.5% of the variance of the fluorescence components, a_{CDOM} 375, and DOC. While all components were positively correlated with factor 1, they were well separated on the axis representing factor 2. This second factor showed the position of fluorescence components along an autochthonous to allochthonous gradient, with components 3, 4, and 8, shown with a_{CDOM} 375 in the lower half of factor 2. Component 1, ascribed to both autochthonous and allochthonous sources, was positioned in the higher part of the lower quadrant compared to the solely autochthonous components. Components 2, 5, 6, and 7, found in the upper quadrant of factor 2, represented the allochthonous portion of the gradient (Fig. 4). Figure 5 illustrates the autochthonous/allochthonous gradient found on axis 2. Despite the fact that the principal component analysis did not include data from the macrophyte excretion experiment, there was a direct negative relationship between the correlation of a given component with factor 2 and its relative contribution to the total FDOM pool leached by the macrophytes. DOC was close to components 6 and 7 in the upper half of factor 2. Concentrations of DOC were strongly correlated with total fluorescence, and this relationship increased when only allochthonous components (2, 5, 6 and 7) were considered (Fig. 6). It decreased considerably when only autochthonous components were considered (Fig. 6).

Lateral variations in FDOM

For clarity, fluorescence components were grouped together and summed as described above, with the "autochthonous" group comprising components 3, 4, and 8, and the "allochthonous" group comprising components 2, 5, 6, and 7. Component 1 is not included in any group since, as described, it appears to originate

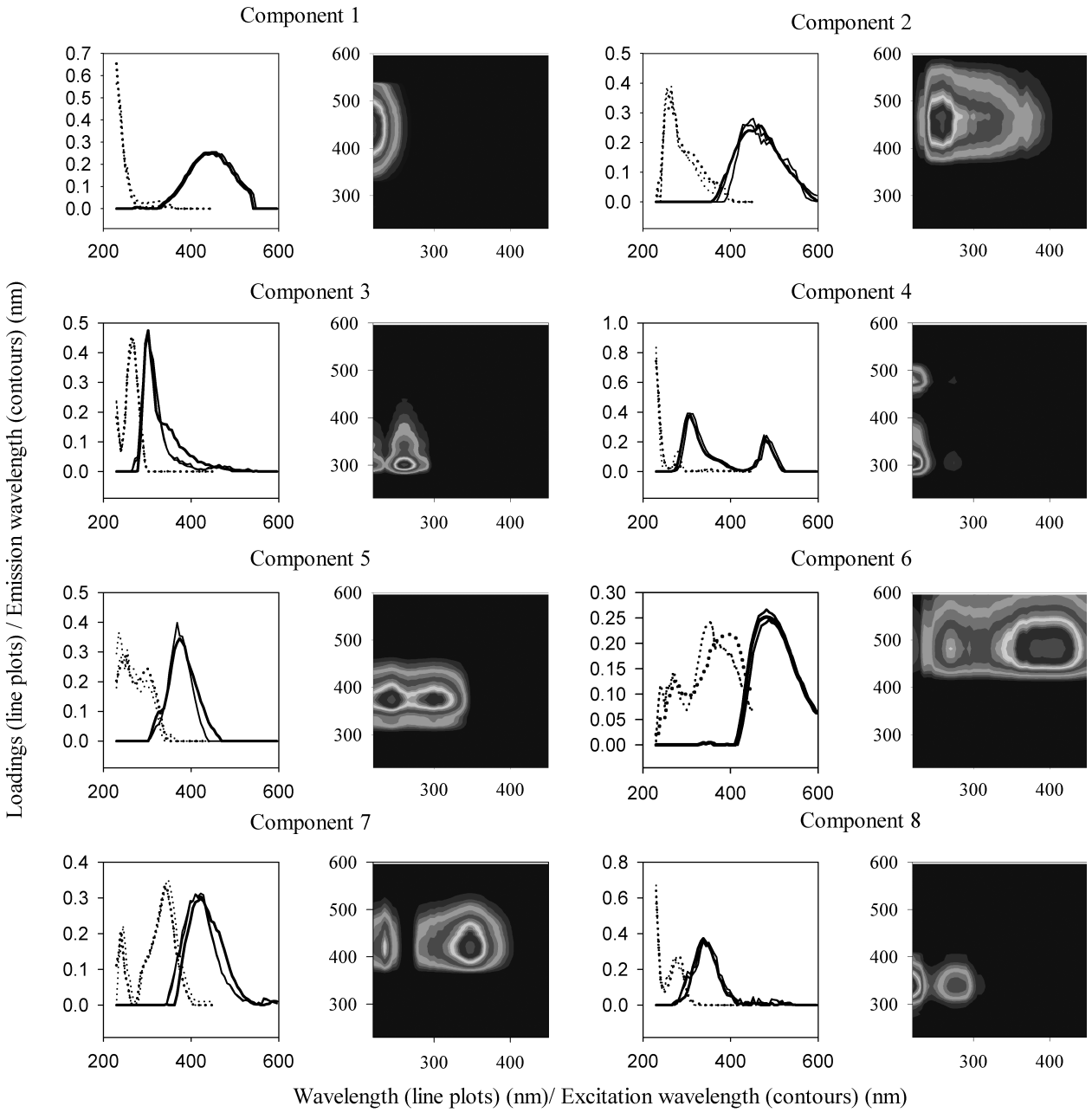

Figure 2. Fluorescence signatures of the eight fluorescence components identified in this study, presented in order of decreasing percent of explained variation. Line plots represent the complete data set (thick line) and split-half validations (thin lines) of the component loadings.

from both sources. Autochthonous and allochthonous FDOM, as well as DOC, achieved maximum abundances in the nearshore zones (Fig. 7). Higher abundances of both autochthonous and allochthonous FDOM were found on the south compared to the north shore. Lateral (shore to shore) gradients are more pronounced for allochthonous components and component 1 compared to autochthonous components and the DOC follows the same overall pattern as FDOM.

Temporal variations of FDOM and macrophyte life cycles

Overall, the allochthonous components showed a stable pattern throughout the 4-month sampling period (Fig. 8). We observed a considerable seasonal shift in the abundance of the autochthonous components (Fig. 8). This shift was especially pronounced for component 4, which was dominant in the submerged macrophyte leaching experiment, and showed a net increase during October and November. These months correspond to the macrophyte senescence

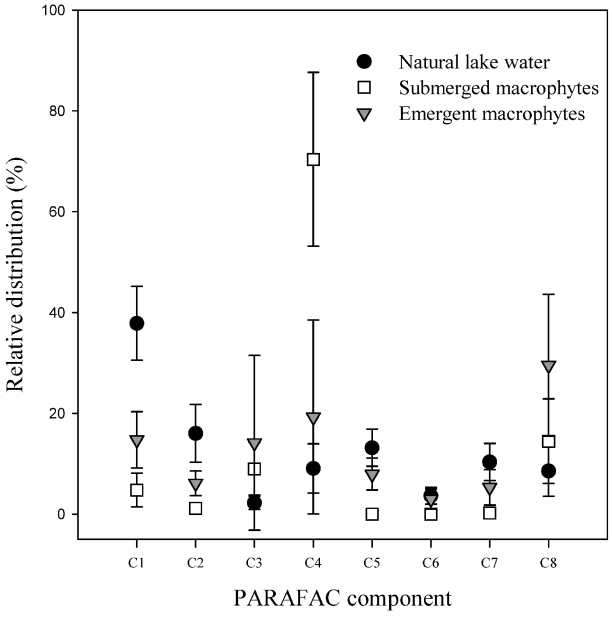

Figure 3. Percent of total FDOM represented by the eight components in the PARAFAC model in natural lake waters, submerged macrophyte leachate, and emergent macrophytes leachate.

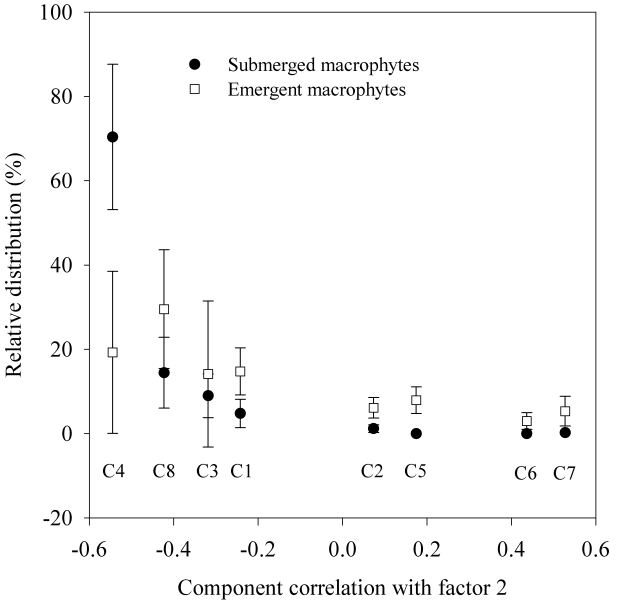

Figure 5. Relationship of the percent contribution to the FDOM in leachate from submerged and emergent macrophyte provided by each component from the PARAFAC model, with the components' correlation with factor 2 of the principal component analysis.

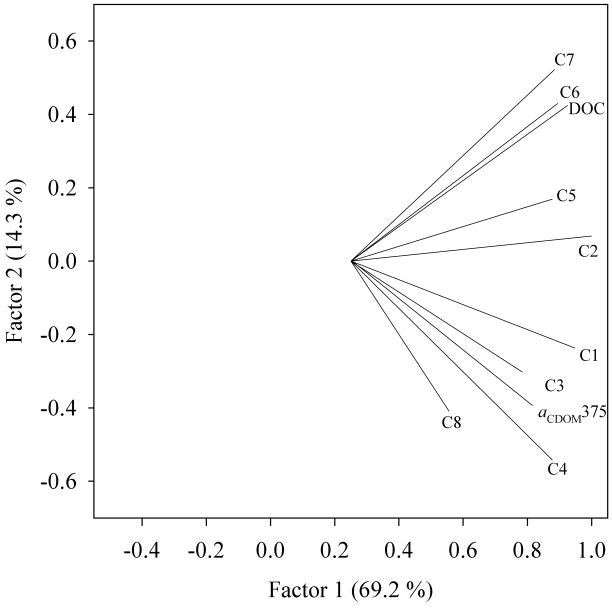

Figure 4. Correlation of DOC, $a_{FDOM}(375)$ and FDOM components with factors 1 and 2 of a principal component analysis peformed only on samples of natural lake water. The first two axes of the analysis explain 83.5 % of the variance. Percent of explained variation shown in brackets.

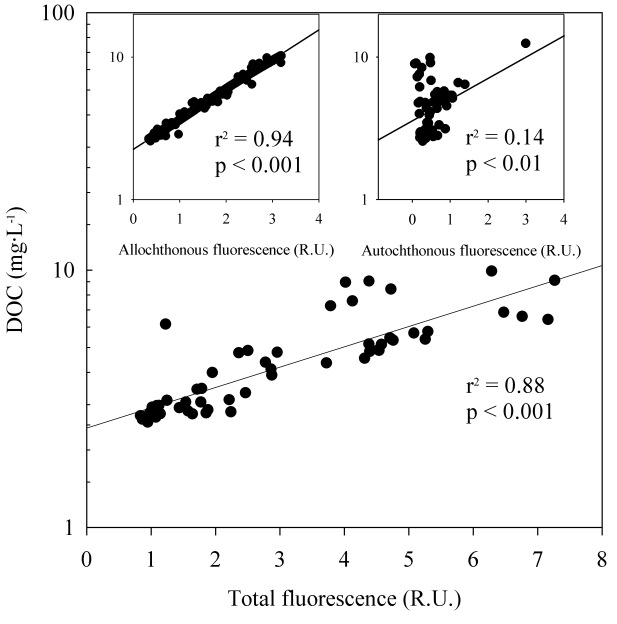

Figure 6. Relationship between DOC and sum of F_{max} of the eight fluorescence components identified in this study; relationship between DOC and sum of F_{max} for allochthonous components 2, 5, 6 and 7 shown in the upper left insert; relationship between DOC and sum of F_{max} for autochthonous components 3, 4 and 8 shown in the upper right

and drifting periods, respectively, in Lake Saint-Pierre. The well-defined, bell-shaped pattern of autumn abundances across the lake was not observed for components 3 and 8. Component 8 was found in higher overall abundances during autumn samplings, but no pattern could be observed for component 3 (Fig. 8).

Discussion

The results of the principal component analysis illustrate that the fluorescence components identified in this study were from various origins. There was a

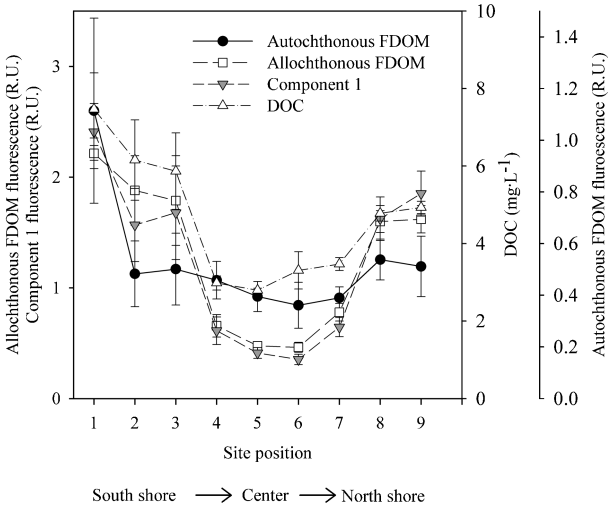

Figure 7. Lateral variations of abundances of allochthonous FDOM (sum of components 2, 5, 6, and 7), autochthonous FDOM (sum of components 3, 4, and 8), component 1, and DOC; R.U. refers to Raman units. Symbols represent averages ± SE for all transects and dates at the same lateral position.

strong link between the correlation of fluorescence components with factor 2 and their respective contribution to the FDOM pool leached from macrophytes in the experiments (Fig. 5). Considering that the principal components analysis did not include data from the macrophyte leaching experiments, the results presented in figure 5 do not represent an inherent autocorrelation but rather suggest that FDOM produced by autochthonous and allochthonous processes in Lake Saint-Pierre possess contrasting optical properties and behave differently in the system, likely due to discrepancies in the sources and fate of these different groups of FDOM.

Components 3, 4, and 8 were the most abundant FDOM constituents leached from macrophytes. The combination of components 3 and 8 corresponds to component 4 from Stedmon and Markager (2005b), a component associated with protein-like fluorescence and algal sources. Component 4 is a combination of components 1 and 4 from Stedmon and Markager (2005b). Their component 1 corresponds to a UV-humic peak associated with both terrestrial and autochthonous sources. The very high dominance of component 4 in our excretion experiments reveals that leaching from macrophytes produces humic substances in addition to protein-like material. In our study site, however, these differ optically from FDOM imported from the terrestrial landscape.

Although most FDOM leached from macrophytes was similar to that excreted from phytoplankton, it

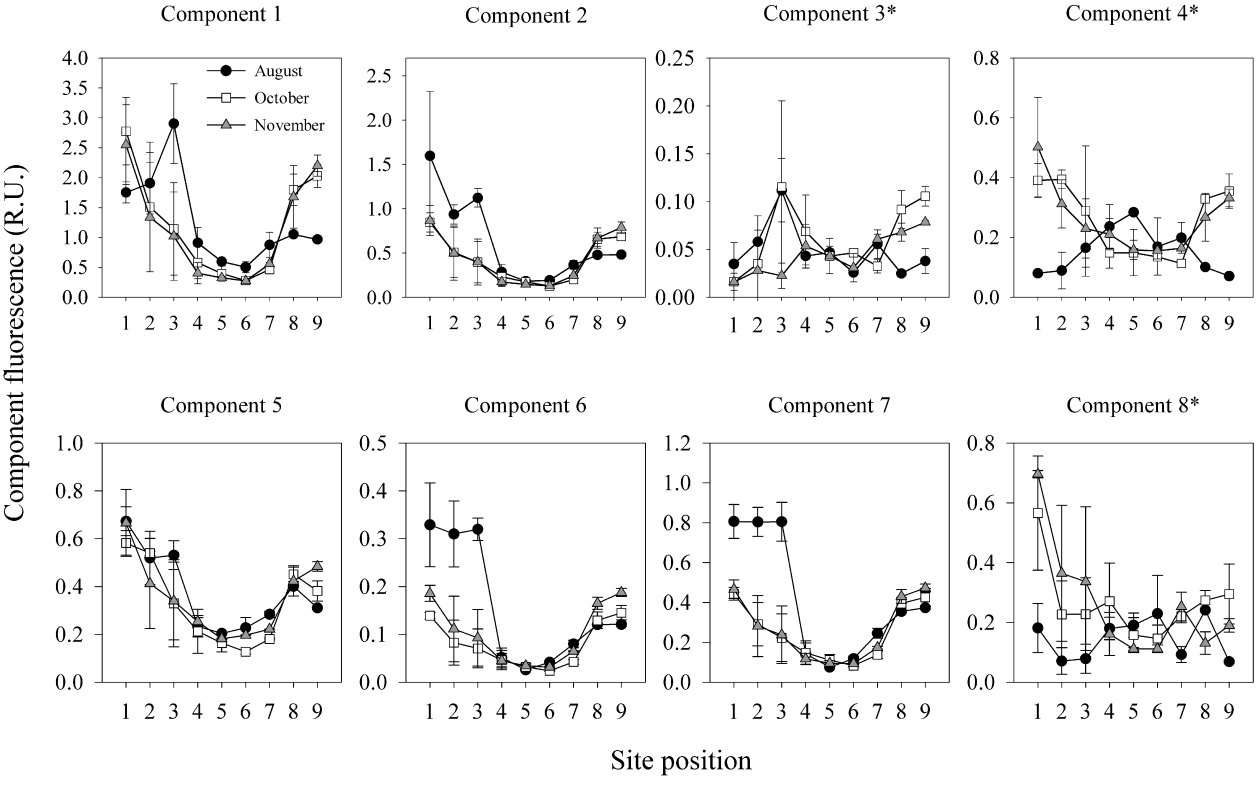

Figure 8. Lateral variations of abundances of FDOM components during periods of maximum abundance (August 18), senescence (October 7), and drifting (November 4) in the macrophyte life cycles. R.U. refers to Raman units. Symbols represent averages across surveys, ± SE, for all transects at the same lateral position. Autochthonous fluorescence components are identified by an asterisk.

also contained certain amounts of humic and fulvic acids similar in fluorescence to those exported from the terrestrial landscape (Fig. 3, Table 1). This is consistent with the higher contribution of components 1, 2, 5, 6, and 7 to the FDOM leached from emergent as opposed to submerged macrophytes (Fig. 3). The former contain higher proportions of structural tissues (Wetzel, 1990; Balogh et al., 2006), which aid in the formation of humic and fulvic acids in soils (McKnight and Aiken, 1998).

The much higher proportions of components 3, 4 and 8 in the macrophyte leaching experiment compared to those found in lake water demonstrate that macrophytes contribute a net autochthonous FDOM input in Lake Saint-Pierre. The production of protein-like and humic material from macrophytes suggests that both macrophytes and their attached epiphytes produce autochthonous FDOM, although this could not be verified due to our experimental design. The fact that the leaching experiments were performed in the dark suggests that photosynthesis is not essential in order for macrophytes, and possibly algae, to be a source of FDOM in the aquatic ecosystem. Also, bacteria most likely played an important role in the production of FDOM during the leaching experiments by decomposing the incubated macrophytes. In any case, FDOM produced under dark conditions in leaching experiments was similar to that associated with photosynthetically active phytoplankton. Leaching from macrophytes is not the only source of autochthonous FDOM in aquatic ecosystems, but the fluorescence signatures of the macrophyte leachate match those autochthonous components previously attributed to phytoplankton excretion (Coble, 1996; Stedmon et al., 2005b). This illustrates that different autochthonous processes can produce FDOM with similar optical properties.

FDOM originating from macrophytes and the terrestrial landscape exhibited distinct optical properties in Lake Saint-Pierre, but this could reflect a different degree of degradation or a time lag between the formation of FDOM and its arrival in aquatic ecosystems. Fellman et al. (2008) identified protein-like fluorophores in appreciable abundances in forest soils. The authors also found that these fluorophores were the most labile compared to other FDOM components, suggesting that protein-like material in soils might be decomposed by bacteria prior to exportation to aquatic environments. This could partly explain why allochthonous DOM has been associated with recalcitrant humic and fulvic molecules while algae, bacteria, and, in this study, macrophytes are associated with freshly produced autochthonous, protein-like material. Our experimental design did not allow discrimination between a direct (leaching, excretion) or indirect (habitat for epiphytes, organic substrate for bacterial decomposition) contribution by macrophytes to FDOM. The incubation conditions, however, were similar to a natural environment (except for light conditions, as discussed earlier) where production and consumption of DOM co-occur. Assuming that consumption of FDOM by bacteria in the leaching experiments was present and representative of natural conditions, we conclude that macrophytes contribute to the standing stock of FDOM, as measured by fluorescence analyses, in Lake Saint-Pierre. However, the very strong correlation between DOC and allochthonous components, as opposed to autochthonous components (Fig. 6), and the position of DOC in the top of the upper quadrant on factor 2 of the PCA illustrates that DOC concentrations in lake Saint-Pierre are mainly controlled by inputs of allochthonous DOM, as opposed to leaching from macrophytes or other potential autochthonous sources.

Consistent with previous works (Stedmon and Markager, 2005; Cory and McKnight, 2005; Ohno and Bro, 2006; Fellman et al., 2008), component 1 represented the most abundant FDOM group in our study site. Along with appreciable proportions of component 1 in the macrophyte leaching experiments, its position on factor 2 (Fig. 4) illustrates that both autochthonous and allochthonous inputs of FDOM determine its concentration in natural waters. Furthermore, the higher abundances of component 1 in natural water compared to that in leaching experiments suggest the presence of a non-macrophyte, most likely terrestrial (Stedmon and Markager 2005a), source of this component. If macrophytes were the only source, one would expect lower concentrations of component 1 in natural water because additional inputs of FDOM arriving from tributaries would gradually diminish the proportion of component 1 in the total FDOM pool.

The FDOM characteristics in Lake Saint-Pierre were influenced by the connectivity with the floodplain and inflowing tributaries, each draining its respective catchment. In the nearshore zone, where allochthonous FDOM concentrations reached their maxima, the tributaries drain large catchments that are heavily impacted by human activities such as agriculture (Frenette et al., 2006) and flow directly into the fluvial lake. Water masses in the center of the lake (positions 4, 5, and 6), where the lowest amounts of allochthonous FDOM were found, originate from the Ottawa River and Lake Ontario, both situated over 250 km upstream (Frenette et al., 2006); Lake Ontario's hydraulic residence time is around 6 years. Recent findings showed that, in systems with high residence times, concentrations and bioreactivity of

FDOM are markedly lower at the outlet compared to the inlet (Mari et al., 2007). Similarly, rivers carry smaller quantities of FDOM when a headwater lake is situated upstream because of in-situ processing of humic and fulvic acids (Larson et al., 2007). Our results, therefore, suggest that the concentration and composition of allochthonous FDOM in Lake Saint-Pierre is a function of a) DOM loading from the floodplain and its tributaries, and b) in situ transformation of DOM during transport from source waters to Lake Saint-Pierre. Thus, we expect that tributaries deliver large quantities of young allochthonous FDOM, which will likely be more bioreactive compared to that found in the older water masses at the center of the lake.

Autochthonous FDOM represented roughly 20 % (averaged for all samplings) of the total FDOM pool in Lake Saint-Pierre based on the fluorescence measurements. The distribution of autochthonous FDOM was strongly linked to the distribution of macrophytes (Jean Morin, unpublished data), to the depth and phosphorus patterns in the system (Hudon and Carignan, 2008) and to primary productivity patterns (Vis et al., 2007). Although the lateral distribution of autochthonous and allochthonous FDOM components were somewhat similar with maxima in the nearshore zones (Fig. 7), our attribution of a fluorescence component to an autochthonous or allochthnous origin is consistent with its presumed source, i.e. primary production or input from tributaries or the floodplain. The principal components analysis (Fig. 4) further illustrated the contrasting distribution of the different FDOM components, which was explained by differences in their sources, as shown in figure 5. The increase in autochthonous FDOM during October and November suggests that senescence, and thus decomposition of macrophytes, also constitutes an important input of autochthonous FDOM in Lake Saint-Pierre and, potentially downstream, because of the autumn drift of dead plants with advected water masses.

Even though macrophytes do not represent a main carbon source for herbivores or direct grazers (Miller, 2004), they contribute strongly to the detritivores' food web through carbon and nutrient cycling and by supporting bacterial consumers. Macrophytes are major constituents of freshwater and marine wetlands and dominate in shallow and productive environments such as fluvial Lake Saint-Pierre. These plant communities are largely influenced by factors such as water level (Hudon et al., 2005) and nutrient enrichment (Hudon, 2004), and thus, ultimately, by human activities. Along with increasing eutrophication of inland waters, the impact of macrophytes as a major carbon source for microbes is likely to increase in years to come as their abundances and distributions grow.

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