ABSTRACT. – Stable carbon isotopes are increasingly used to estimate the relative contribution of phytoplankton and periphyton towards secondary production in aquatic food webs. This approach, developed mostly through studies of deep stratified lakes, remains to be evaluated in the context of large rivers, where factors such as short water residence time, little stratification, and variable turbidity may affect carbon fractionation by primary producers. We used invertebrate filterers and grazers as integrators of isotopic ratios of phytoplankton and periphyton, respectively, in twelve stations from a large (35 km) fluvial lake of the Saint-Lawrence River, Québec, Canada. We found strong but variable differences in Δδ13C, ranging from 1 to 7 ‰, between grazers and filterers collected at the same sites. Following an experimental approach we then showed that the light regime, known for influencing isotopic fractionation from dissolved inorganic carbon, accounted for very little variability in the isotopic ratio of periphyton. On the other hand, field data showed that the isotopic difference between filters and grazers was strongly related to spatial variation in the relative abundance of phytoplankton and periphyton within the lake. This study showed that the basis of benthic food web production in a fluvial lake is spatially highly variable and can be efficiently quantified with carbon isotopes. Our results revealed the existence of a complex spatial mosaic ranging from an almost complete trophic dependence on phytoplankton to an important assimilation of non-sestonic sources.
ascribed to two physical processes ultimately affecting the \( \delta^{13}C \) of algae. First, compared to phytoplankton, periphytic algae grow in a benthic environment with relatively low turbulence, resulting in a thicker boundary layer near the cell surface. This limits the diffusion of C into the cell resulting in a decreased isotopic discrimination during photosynthesis (Smith & Walker 1980, Heckey & Hesslein 1995). A second important process leading to more negative \( \delta^{13}C \) in phytoplankton in the pelagic zone is the recycling of respiratory dissolved inorganic carbon (DIC) accumulated in the deeper strata of the lake. This depleted carbon can be in part assimilated by phytoplankton and contributes to increasing the isotopic differentiation between pelagic planktonic and littoral periphytic algae (Rau 1978). Diffusion of very negative \( \delta^{13}C \) originating from hypolimnetic methane emission followed by oxidation may also contribute to the depletion in phytoplankton \( ^{13}C \) observed in some lakes (Ravinet et al. 2010).

Thus isotopic discrimination between food chains based on benthic vs pelagic primary producers is commonly observed in stratified lakes (France 1995a, Sierszen et al. 2006) and this pattern has been exploited to evaluate the relative importance of benthic vs pelagic production in these ecosystems (Heckey & Hesslein 1995, Vander Zanden & Vadéboncoeur 2002) and applied to evaluate the flow of contaminants associated to these alternate trophic paths (Eagles-Smith et al. 2008). However, the applicability of this isotopic approach to the study of food webs in large rivers can be a priori questioned on the grounds of three observations. First, large shallow rivers typically have a well-mixed water column resulting in a vertical mixing of \( \delta^{13}C \) of DIC. Unlike in deeper lakes, there is no pelagic zone distanced from the littoral zone and consequently phytoplankton and periphyton should be using the same source of DIC with no difference in \( \delta^{13}C \). Secondly, while current velocity may be reduced in certain nearshore areas and embayments of rivers, the occurrence of flowing waters in rivers near bottom may contribute to alleviate the effect of the boundary layer on fractionation by periphyton hypothesized to occur in lakes (Hecky & Hesslein 1995). This would then result in a more negative periphyton \( \delta^{13}C \) in rivers, closer to phytoplankton \( \delta^{13}C \), opposite to what is observed in lakes. Indeed, field as well as experimental work has shown that water velocity greatly increases C isotopic discrimination from DIC by periphyton (Finlay et al. 1999, Trudeau & Rasmussen 2003). Thirdly, diminished isotopic discrimination between phytoplankton and periphyton could also be caused by variable fractionation in periphyton as a function of light levels. Turbidity related to suspended organic or inorganic matter, a common situation in rivers, decreases the quantity of light available for the photosynthesis of benthic algae. This causes a reduction in the C demand, resulting in an increase in isotopic fractionation from DIC (Laws et al. 1995). Under light stress, periphyton could therefore acquire a more negative \( \delta^{13}C \) closer to that of phytoplankton.

The aim of this study is to examine if \( \delta^{13}C \) can be used to distinguish phytoplankton-based from periphyton-based food chains in a large fluvial lake. To achieve this goal, we used the \( \delta^{13}C \) of grazers and filterers as integrators of the \( \delta^{13}C \) signal of periphyton and phytoplankton, respectively (Post 2002). We show that the isotopic differentiation between these consumers is highly variable within the fluvial lake. This result could be brought by at least two mechanisms: first, variable fractionation by primary producers from their carbon source(s) and transfer of this signal up the food chain and secondly, pelagic-benthic coupling which would lead to the mixing of food sources. To investigate these two mechanisms, we used (i) an experimental approach to determine if the light regime, known for influencing isotopic fractionation from DIC (MacLeod & Barton 1998), accounted for the variability in the isotopic ratio of periphyton, and (ii) field data to determine if isotopic difference between filterers and grazers was related to spatial variation in the relative abundance of phytoplankton and periphyton within the lake.

METHODS

**Study area:** Lake Saint-Pierre (LSP) represents the largest (480 km²) and the last fresh water basin of the St. Lawrence River before the estuary. Since 2000, the UNESCO have classified the LSP as an ecological reserve of the biosphere, due, in part, to its important floodplain (18 km²) and biodiversity (288 bird species and 83 fish species) (Langlois et al. 1992). Having an average depth of 3 m, it has an important width/depth ratio reducing the horizontal mixing of water, resulting in the persistence of three main water masses (Frenette et al. 2003). Because of its morphometry, LSP offers a variety of colonizable substrates for benthic algae and the distinct characteristics of the water masses confer important spatial heterogeneity in environmental conditions. In July and August 2006, we sampled twelve stations; ten in the LSP’s slackwaters and two as near as possible to the central water mass (Fig. 1). Each station consisted of five sampling sites distributed in a cross pattern; the four peripheral sites were 150 m away from the central site.

**Water characteristics:** At each station, we measured vertical profiles of turbidity using a multiprobe (Yellow Spring Instruments, 650). Light profiles were performed using a spectroradiometer (PUV2545, Biospherical Instruments). Surface water samples, one per station, for nutrient analyses (total nitrogen (TN) and total phosphorus (TP)), were collected in acid-washed polyethylene containers. Analyses of TN were done by reduction of nitrates to nitrites by cadmium followed by spectrophotometry (Standard Methods 1998). Analyses of TP were done by hydrolytic transformation of organic phosphorus, by persulfate...
iphyton ratio (PPr) was calculated as:

\[ PPr = \log (\text{phyto} / \text{peri}) \]

where [phyto] and [peri] correspond to the concentration in Chl a in mg m\(^{-2}\) phytoplankton and periphyton, respectively.

**Primary producers:** Phytoplankton and periphyton biomasses at each station were determined, respectively, by the concentration in Chlorophyll a (Chl a) in water samples and on artificial substrates. Four litres of water from the first 1.5 m were sampled at each station (we introduced 1.5 m of an open PVC tube in the water and closed the top extremity to sample, by suction, the entire water column) for phytoplankton analyses. Matter covering four artificial substrates (10 by 10 cm porous ceramics plates) at the 5 sites of each station was collected with a tooth brush, after a minimum of one month of growth (artificial substrates at the 5 sites of each station were set on June 12 and were collected between the 4\(^{th}\) and 12\(^{th}\) of July (first sampling period), and between the 17\(^{th}\) and 28\(^{th}\) of August (second sampling period)).

In the laboratory, a homogenized fraction of each sample was then collected on Millpore APFF filters (0.7 \(\mu\)m) until the filters were visibly clogged. They were then frozen at -20 °C until Chl a analyses. Filters were sonicated in cold acetone (90 %) and extraction continued in the dark for 24 hours at 4 °C. After centrifugation (5000 rpm, 5 min), we used a Turner Design fluorometer (model 10-005R) to measure Chl a (Parsons, Maita & Waterlow 1984). We averaged phytoplankton and periphyton biomasses for the 5 sites at each station/date.

As suggested by Vadeboncoeur et al. (2002), values of Chl a were transformed into mg m\(^{-2}\) by multiplying volumetric concentration (mg Chl a m\(^{-3}\)) by depth (m). A Phytoplankton to Periphyton Ratio (PPR) was calculated as:

\[ PPR = \log (\text{phyto} / \text{peri}) \]

and boric acid into ortho-phosphates followed by spectrophotometry (Standard Methods 1998).

We also sampled each station for \(\delta^{13}C\) of dissolved inorganic carbon (DIC-\(\delta^{13}C\)) in 2007. Water was sampled near the surface with a syringe and was immediately filtered on a 0.22 \(\mu\)m syringe filter in an amber glass bottle. The bottle was completely filled and capped with a double septum, kept cold (4 °C) and syringe filter in an amber glass bottle. The bottle was completely filled and capped with a double septum, kept cold (4 °C) and sent to GG Hatch Isotope Lab (University of Ottawa, Canada) for \(\delta^{13}C\) analyses the following day.

Primary consumers: Zoobenthos was collected at each station using a biological dredge (mesh size of 1 cm) and the contents of the dredge were kept cold in the field until frozen in the laboratory. We defined grazers as benthic non-filtering primary consumers. Those included an amphipod (Gammarus fasciatus Say) which can consume fresh benthic algae, deposited material and detritus (Liméen et al. 2005) and two snail species (Goniobasis livescens Menke and Planorbella trivolvis Say). For the pelagic food web, three bivalves (filterer organisms) were selected: Elliptio complanata Lightfoot, Lampsilis radiata Barnes and Dreissena polymorpha Pallas. We also captured Bithynia tentaculata Linne and Viviparus georgianus Lea. These gastropods are able to feed simultaneously on benthic and planktonic algae (Brendelberger & Jurgens 1993, Declerck 1995) and are considered separately.

For G. gammarus whole individuals were used, while only the soft body of the gastropods and the posterior delivery muscle of the bivalves were used. Thereafter, the samples were dried (3 days at 60 °C), crushed, then acidified drop by drop (HCl 1mol L\(^{-1}\)) to remove carbonates according to the method of Jacob et al. (2005). The samples were dried again (three days at 60 °C) and 0.20 ± 0.02 mg were weighed in a tin cup and sent for isotopic analyses. Stable isotopes of C were analyzed with a Finnigan Delta mass spectrometer at the Stable Isotopes in Nature Laboratory (SINLAB) (New Brunswick, Canada). Isotopic ratios are expressed in the usual δ notation, the deviation in ‰ being compared to a reference standard, Pee Dee Belemnite:

\[ \delta^{13}C = \left[ \frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right] \times 1000; \]
\[ R = ^{13}C / ^{12}C \]

Isotopic fractionation of benthic algae: An experiment in a semi-controlled medium was carried out to examine the relationship between periphyton \(\delta^{13}C\) fractionation and light intensity. During summer 2007, we installed a series of containers on a floating platform on lake Joseph (Canada), an eutrophic lake (Simoneau et al. 2004). This set up consisted of a pump that constantly supplied lake water to four containers, each containing four artificial substrates (porous ceramics plates 10 by 10 cm). Substrates were always covered by 5 cm of water. Above each substrate, the lids were perforated and covered with screen filters letting light pass at 4, 6, 15 and 31 % of the incidental light. Filters were selected to reflect the incidental light calculated at the bottom of our twelve stations in LSP.

Periphyton was collected as described above after 1 month of growth. A portion of each sample was filtered and immediately analyzed for Chl a. The other portion was reserved for density fractionation in order to separate the algal and detritus components (Hamilton et al. 2005). The algal fraction was then collected on filters (Millipore APFF (0.7 \(\mu\)m)) rinsed beforehand with acid (0.1 N) and pre-dried (230°C, during six hours). The filters were then frozen. Before isotopic analyses, the filters were rinsed with acid in order to eliminate carbonates and then dried following Jacob et al. (2005).

**Statistical analyses:** \(\delta^{13}C\) of filterers and grazers species were analyzed using a paired t test procedure with a Bonferonni
adjustment in order to evaluate differences between isotopic values of species. The semi-controlled experiment results (Chl a and δ13C) were analyzed using the ANOVA procedure with a Tukey post hoc test. An ANCOVA was used to evaluate the homogeneity of slope and intercept between the two regressions linking the Δ13C (difference between δ13C of filterers and grazers) and PPR. We use $p < 0.05$ as significance criterion for all our statistical analyses.

RESULTS

Limnological characteristics of sample stations

The twelve stations were highly variable with respect to physical and chemical characteristics (Table I). The turbidity for the two sampling periods varied between 0.3 at station 4 and 121.3 NTU at station 8 and the percentage of the incident light reaching the bottom at each station varied accordingly between 0.2 to 37.4 %. The concentration of nutrients also varied between the 12 stations (TN ranged from 0.05 to 1.49 mg L$^{-1}$ and TP ranged from 7.4 to 165.4 µgP L$^{-1}$). In 2007, δ13C-DIC varied between –1.6 (11) and –12.9 ‰ (8) among stations (Table I).

Selection of isotopic integrators

There were no difference between the δ13C of the filterers (mean pairwise differences ranging from 0.16 to 0.95; $p > 0.7$ in all cases), indicating that the selected species are consistent integrators of sestonic sources of C. We report thereafter average δ13C values of filterers present at each station/date.

δ13C of B. tentacula and V. georgianus were significantly lower than the other grazer species collected at the same station (mean paired differences ranging from –1.8 to –7.1; $p = 0.016$ and 0.014, respectively). This isotopic shift confirmed the capacity of these organisms to feed on suspended algae (Brendelberger & Jurgens 1993, Declerck 1995). We therefore excluded B. tentacula and V. georgianus as indicators of the periphytonic carbon source.

In the case of G. fasciatus, G. livescens and P. trivolvis, the mean differences in δ13C among these species ranged from 0.6 to 2.7 ($p > 0.8$). Thus, δ13C values presented here as indicators of the benthic food web are the averages of δ13C of G. fasciatus, G. livescens and P. trivolvis found at each station/date.

Isotopic differentiation between pelagic and benthic primary consumers

In LSP, grazers and filterers δ13C was extremely variable ranging respectively between –28 to –16 ‰ and –32 to –19 ‰, therefore resulting in an important overlap between the δ13C of filterers and grazers (Fig. 2A) contrasting pelagic seston feeders to non-filtering primary consumers and higher trophic level organisms captured in the littoral zone (Fig. 2B). Using averages by station/date revealed a significant correlation between δ13C of grazers and filterers ($p < 0.001$) and therefore removed spatial/temporal variation in baseline isotopic values. The slope of that relationship was not significantly different from one ($t = 1.88, df = 17, p > 0.05$). Grazers were generally enriched in 13C compared to filterers. However, this enrichment was variable ranging from 1 to 7 ‰ (Fig. 3).

Table I. – Averages of July and August limnological characteristics for the 12 stations: depth, turbidity (Turb), coefficient of light attenuation of Photosynthetic Available Radiation ($K_d$), sum of nitrates and nitrites (TN), total phosphorus (TP), concentration of Chl a in seston (Phyto), concentration of Chl a collected on artificial substrates (Peri), C isotope values of the total dissolved inorganic carbon (δ13C-DIC) and the percentage of grazers’ carbon provided by periphytic algae (grazer’s reliance on periphyton). *Samples for DIC were collected in August 2007.

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<th>$K_d$</th>
<th>TN (mg/L)</th>
<th>TP (µgP/L)</th>
<th>Phyto (µg L$^{-1}$)</th>
<th>Peri (mg m$^{-2}$)</th>
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Isotopic fractionation of benthic algae

Periphyton grown under high light intensity (31 % of incident light) showed the highest concentration biomass ($F = 34.94; p < 0.001$) (Fig. 4A) and isotopic fractionation significantly increased by about one 1 ‰ under low light intensity (4, 6 and 15 %) ($F = 16.75; p = 0.001$), resulting in more negative δ¹³C periphyton (Fig. 4B).

Contributions of phytoplankton and periphyton to primary consumers

Phytoplankton biomasses varied by approximately an order of magnitude (1.7 to 12.4 μg L⁻¹) while periphyton varied by three (0.03 to 8.2 mg m⁻²) (Table I). Phytoplankton to Periphyton Ratio (PPR) varied from −1 to 2.3 (Fig. 5). Therefore, on an areal basis, the biomass of phytoplankton relative to that of periphyton varied by more than three orders of magnitude among our stations. Variation in ∆δ¹³C (difference between δ¹³C of grazers and filterers) was related to PPR ($r^2 = 0.80; p < 0.001$) (Fig. 5). Analysing separately the two species known to be facultative grazers/filterers (B. tentacula and V. georgianus) resulted in a similar negative slopes between ∆δ¹³C and PPR (ANCOVA test for homogeneity of slopes; $f = 0.655; p > 0.05$), but with a significantly lower intercept (ANCOVA; $F = 43.278; p < 0.001$).

DISCUSSION

Phytoplankton biomass varied by an order of magnitude within LSP, ranging from oligotrophic (e.g. 1.7 μg Chl a L⁻¹, in station 4, Table I) to eutrophic levels (12.5 μg L⁻¹, station 9) (Wetzel 2001). Nutrient limitation in some areas of LSP may contribute to explain some of this spatial variation in productivity (Hudon et al. 2009). However this range in algal biomass is nonetheless limited compared to the wide range of phytoplankton biomass reported for rivers (< 1 up to > 400 μg Chl a L⁻¹, Wehr & Descy 1998). Similarly, even if periphyton biomass ranged over three orders of magnitude in LPS, our values were relatively low in comparison to streams with high nutrient loadings where maximum periphyton biomasses can range up to 300 to 400 mg Chl a m⁻² (Stevenson et al. 1996). However, the biomass of periphyton relative.

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to that of phytoplankton (PPR) ranged from –1.1 to 2.4 within the fluvial lake. This indicates that in some areas, periphyton is about ten times more abundant than phytoplankton and that in others phytoplankton is about three hundred times more abundant than periphyton. Such variation in the abundance of phytoplankton relative to that of periphyton may be related to the relative productivity of these algal components observed in data compiled by Vadeboncoeur et al. (2002). Their observed ratios ranged from periphyton being about five times more productive than phytoplankton in some systems to phytoplankton biomass exceeding that of periphyton by a factor of about forty times in others.

A study done by Fry (2002) along a δ13C-DIC gradient ranging from –10 to –2 ‰, showed a relationship between the δ13C of the DIC and bivalves. Similarly, the important range of primary consumers δ13C reported here in LSP (e.g. –32 to –19 ‰, Fig. 2A) for bivalves, which is similar to that reported in a global survey (Finlay 2001) could be related to spatial variability in the δ13C-DIC available to primary producers. The variation in δ13C-DIC that we observed in LSP (–1.6 to –12.9 ‰, Table I) could be explained by the inputs of low δ13C-DIC tributaries contrasting with high carbonate and high δ13C-DIC waters from the Great Lakes (Barth & Veizer 1999, Yang et al. 1996). The δ13C of filterers greatly overlapped with those of grazers (Fig. 2) and this was in a large part the result of the spatial variation in baseline δ13C. However, after correcting for this spatial variation by matching filterers to grazers by station, substantial variability in Δδ13C was still observed among sites (Fig. 5). Thus the scope for differentiating isotopically grazers from filterers was often reduced in many areas of LSP. This result contrasts with the comparative data summarized by France (1995b) (Fig. 2B), where a very small overlap in δ13C was observed between littoral and pelagic consumers and the range to differentiate these two functional groups averaged 7 ‰. However, these results were based on isotopic ratios obtained largely from deep oligotrophic lakes which are subjected to vertical variation in the δ13C-DIC (Rau 1978), increasing the likelihood of isotopic differentiation between phytoplankton and inshore periphyton.
In the absence of strong stratification in shallow lakes and rivers, both phytoplankton and periphyton should be using the same pool of DIC. Therefore, vertical variation in $\delta^{13}C$-DIC in large rivers and fluvial lakes should not be a driving factor controlling the isotope differentiation between primary producers. However, the fractionation effects by boundary layer phenomena observed in periphyton could be a factor in shallow water bodies as well as in deeper one, potentially explaining shift between $\delta^{13}C$ of grazers and filterers observed in the present study (Fig. 3).

The percentage of incident light reaching the bottom in our twelve stations in LSP varied between 0.2 to 37.4 % (Table I). This range of variation in light intensity caused a significant but modest fractionation of periphyton from DIC in our experiment. However, the maximum potential fractionation linked to light levels observed in this experiment (1 %, Fig. 4B) is insufficient to explain the among-stations variation in $\Delta\delta^{13}C$ (Fig. 5). In a field experiment, MacLeod & Barton (1998) showed that under different light regime conditions (100 and 10 % of the incident light), the $\delta^{13}C$ of periphyton varied of about 3 ‰ during the growth season. However, their experimental light regime reached higher levels than the light conditions observed at the bottom of LSP and in our experiment. Therefore, fractionation by periphyton related to variable light regime is not likely to be an important factor explaining variation in the isotopic ratios of grazers in LSP.

Another possible mechanism explaining the variability of $\Delta\delta^{13}C$ among sites is the mixing of sources of C available to filterers and grazers. The negative relationship between $\Delta\delta^{13}C$ and the PPR indicated that when periphyton was dominant, grazers and filterers have distinct $\delta^{13}C$ values and conversely, when phytoplankton was dominant, grazers and filterers have similar isotopic ratios. This suggests that in an environment dominated by periphyton, grazers and filterers feed on distinct C source. However, in an environment dominated by phytoplankton, both grazers and filterers depend almost entirely on phytoplankton. This convergence of isotopic ratios between those two functional feeding groups may be explained by a pelagic-benthic coupling caused by the sedimentation of phytoplankton made available for grazers. Resuspension of benthic algae or deposited phytoplankton (Carrick et al. 1993) in large shallow systems like LSP could also contribute to the mixing of phytoplankton and periphyton. Vadeboncoeur et al. (2003) obtained similar results in shallow productive lakes where benthic primary consumers had $b^{13}C$ close to those of phytoplankton primary producers. They suggested that domination in the biomass of planktonic algae caused a diet change in grazers, shifting from periphyton to phytoplankton. Such changes in trophic relationships could be related to grazing on deposited phytoplankton or to modifications of grazer feeding systems. Our result suggests that both mechanisms could be at work in fluvial lakes. Indeed, the relation between $\Delta\delta^{13}C$ of grazers able to modify their feeding system to consume suspended planktonic algae (facultative grazers such as *B. tentacula* and *V. georgianus*) and PPR is similar to that of the grazers (Fig. 5). However, for a same PPR, values of $\Delta\delta^{13}C$ of the facultative grazers were always smaller than those of presumed to be obligate grazers. This indicates that even in an environment dominated by periphyton, facultative grazers still filtered suspended phytoplankton. This result is coherent with the study of Tashiro & Colman (1982) on *Bithynia tentaculata* which showed that the net energy gain of grazers is higher when they feed on suspended phytoplankton, a potential advantage relative to other benthic invertebrates.

To estimate the variation in the relative importance of periphyton vs phytoplankton to primary consumers among our sites we first assumed that filterers fed exclusively on phytoplankton and secondly, that $\delta^{13}C_{\text{periphyton}} - \delta^{13}C_{\text{phytoplankton}}$ was equal to 7 ‰ (estimated by the greatest within-site difference in $\delta^{13}C$ observed between filterers and grazers in LSP). Grazer reliance on periphytic carbon can then estimated following a simple mixing model as:

\[
\% \text{ dependence periphyton for grazers} = \Delta\delta^{13}C / 7 \%
\]

The percent reliance of grazers on periphyton was variable, ranging from 96 (station 4) to 27 % (station 9, see Table I). The average of the 12 stations/dates shows that grazers rely at 65 % on periphyton and 35 % on phytoplankton, indicating substantial pelagic-benthic coupling.

In conclusion, our results suggest that stable isotopic data may be used to trace the relative contribution of phytoplankton and periphyton to consumers in large shallow rivers. Our LSP data suggest that large rivers are constituted by a mosaic of areas where patterns of carbon flows to consumers range from a dominant contribution of phytoplankton to not only filterers, but grazers as well, to a partitioning of phytoplankton and periphyton use among different consumers in areas where periphyton was more important. We showed that in such an ecosystem that the carbon food source of grazers can vary from a strong reliance on periphyton (96 %) to an important (73 %) dependence on phytoplankton in some areas. A similar pattern was observed in the upper Mississippi River where Delong & Thorp (2006) noted that collector-gatherers/detritivores or scrapers had isotopic signatures corresponding to that of planktonic algae. Lastly, our results show that the difference in $\delta^{13}C$ between filterers and grazers was strongly related to the variation in the relative abundance of phytoplankton and periphyton. These spatial patterns $\delta^{13}C$ are coherent with an important role played by algae in this food web. They therefore strongly support the River Production Model of Thorp et al. (1998) which maximizes the importance of local autochtonous production in large river ecosystems rather than the contribution of upstream processing or lateral terrestrial inputs during flooding emphasized by other models (Vannote et al. 1980, Junk, Bayley & Sparks 1989).
ACKNOWLEDGMENTS. – We like to thank JF Déry, C Lavallée, M Paquette Perreault, P Thibeault and A Veillette for their work in the field. This work was supported by the FQRNT and NSERC to G Cabana and JJ Frenette.

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Received on June 7, 2016
Accepted on August 14, 2016
Associate editor: N Coineau

Vie Milieu, 2016, 66 (3-4)