

Université de Montréal

**Réponse de la communauté de mollusques aux
perturbations physiques et chimiques dans un grand lac
fluvial (Lac Saint-Pierre, Fleuve Saint-Laurent, QC)**

par

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Ce mémoire intitulé:

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Résumé

Les mollusques sont des indicateurs de perturbations anthropiques et environnementales. Ce groupe de macroinvertébrés représente en outre une source importante de nourriture pour les poissons et les oiseaux aquatiques du littoral. Les hypothèses de cette étude sont que la communauté de mollusques est influencée indirectement par les tributaires agricoles et/ou par des variables environnementales (comme la dessiccation et l'exposition aux vagues) puisque ces perturbations sont susceptibles de modifier leurs sources alimentaires et leur habitat. Les indicateurs de la réponse des mollusques aux agents perturbateurs sont la composition, la diversité, la densité, ainsi que la biomasse des espèces. En septembre 2013, des mesures de paramètres physico-chimiques de l'eau ont été réalisées, et des échantillons de mollusques et de végétation aquatique ont été prélevés à 14 sites le long des rives du lac Saint-Pierre (Fleuve Saint-Laurent, Québec, Canada). Le long de la rive nord, les sites fortement exposés à l'action du vent, situés à de plus grandes élévations, affichaient une plus faible densité, biomasse et richesse spécifique de mollusques que les sites de la rive sud, en milieu plus abrité et profond. Les sites physiquement perturbés étaient caractérisés par de faibles biomasses en macrophytes submergés. Les sphaeriidae apparaissent comme des exceptions à ces patrons, montrant une abondance plus élevée aux sites presque dépourvus de macrophytes. Bien que les variables physiques et l'habitat exercent une influence déterminante sur les communautés de mollusques, les gastéropodes et les moules unionidés étaient également affectés par la dégradation de la qualité de l'eau dans le panache des tributaires agricoles. La richesse, la densité et la biomasse des gastéropodes étaient négativement influencées par des

teneurs élevées de matières en suspension et de fer dissous. Les résultats de notre étude montrent que la communauté de mollusques du lac Saint-Pierre est directement affectée par l'émersion périodique, l'exposition au vent, et indirectement par l'effet de ces variables physiques sur les macrophytes qui constituent leur habitat.

Mots-clés

Gastéropodes, moules, sphaeriidae, lac Saint-Pierre, macrophytes, fluctuations du niveau d'eau, exposition aux vent, qualité de l'eau.

Abstract

Molluscs are indicators of anthropogenic and environmental disturbances and constitute an important food source for littoral fish and aquatic birds. The main hypotheses put forward for our study are that the mollusc community is impacted by the agricultural tributaries and/or by physical variables (desiccation, exposure to waves) through changes in food and habitat. The indicators used were mollusc species composition, diversity, density, and biomass. Over the course of two weeks in September 2013, we sampled physical/chemical water variables, collected aquatic vegetation and molluscs at 14 sites on both shores of Lake Saint-Pierre (St. Lawrence River, Quebec, Canada). Sites located at higher elevations, subjected to recent water level fluctuations, and exposed to wind fetch along the north shore, had lower gastropod and unionid mussel richness, density, and biomass than less-exposed sites located at lower elevations along the south shore. These physically disturbed sites were characterized by low biomasses of submerged macrophytes. Sphaerid clams appeared to be notable exceptions to these patterns, showing their highest abundances at sites almost devoid of macrophytes. In spite of the fact that physical and habitat variables exerted a strong effect on mollusc communities, gastropod and unionid mussels were additionally affected by degraded water quality originating from agricultural tributaries. Gastropod richness, density, and biomass were negatively influenced by high levels of total suspended matter and dissolved iron. Our results show that the mollusc community in Lake Saint-Pierre was primarily affected by the direct influence of periodic emersion, wind exposure, and indirectly through the effect of these physical variables on macrophyte habitat.

Keywords

Gastropods, mussels, sphaeriidae, Lake Saint-Pierre, water level fluctuations, wind exposure, macrophytes, water quality.

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Liste des abréviations

ANCY : Ancyliidae

BITH : Bithyniidae

DM : Dry mass

DO : Dissolved oxygen

DOC : Dissolved organic carbon

DREI: Dreissenidae

ELLI : Elliptio

GAST: Gastropod

HYDR : Hydrobiidae

LAMP : Lampsilis

LEPT : Leptodea

LYMN : Lymnaeidae

MOLL : Molluscs

PHYS : Physidae

PISI : Pisidium

PLAN : Planorbidae

PLEU : Pleuroceridae

SPHA : Sphaeriidae

SPUM : Sphaerium

SSPP : Sphaeriidae spp.

STRO : Strophitus

SW : Southwest

TDN : Total dissolved nitrogen

TDP : Total dissolved phosphorus

TN : Total nitrogen

TP : Total phosphorus

TSM : Total suspended matter

UNIO : Unionidae

VALV : Valvatidae

VIVI : Viviparidae

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Chapter 1: General Introduction

Freshwater molluscs are good bioindicators of water quality because of their worldwide distribution, abundance, and key role in the functioning of aquatic ecosystems (Oehlmann & Schulte-Oehlmann 2002). Owing to their relatively large size, limited movement ability or sessile habit, ease of collection and identification, molluscs are ideally suited as indicators of the environmental conditions of the particular sampling location under study.

Gastropod feeding and life history

Most freshwater gastropods graze on periphyton (algae) that cover submerged surfaces such as macrophytes or cobble (Pennak 1989). Periphyton is preferred over macrophytes because the former is easier to scrape (Thorp & Covich 2009). Food is generally brought into the mouth via rasping movements of the radula. Under slight gastropod grazing pressure, periphyton is dominated by filamentous green algae, but more intensely grazed areas are mainly dominated by toxic species such as cyanobacteria (Doremus & Harman 1977). Other freshwater snails are detritivores, feeding on dead plant or dead animal material. However, all gastropods may occasionally ingest carrion or small invertebrates associated with periphyton (Bovbjerg 1968). Some gastropods feed on algae at the water surface by floating upside down while being supported by surface tension (Thorp & Covich 2009). Certain prosobranchs, such as *Bithynia tentaculata*, may alternate between grazing and filter feeding when suspended food particles are abundant in the water column (Tashiro & Colman 1982).

Freshwater gastropods are characterized by different types of life histories, which have been used as a basis of their classification into the pulmonates and the prosobranchs (also known today as the caenogastropods). The pulmonates possess a “lung” like structure, which enables them to obtain oxygen from the air when they come to the water surface (Pennak 1989). The prosobranchs, on the other hand, use an internal gill called a ctenidium, to breathe dissolved oxygen in the water.

Freshwater pulmonates, such as physids, are hermaphrodites: every individual has both male and female organs for reproduction. In contrast, the prosobranchs are dioecious meaning the sexes are separate. In this group, the male genital pore is usually situated near the base of the right tentacle, at the end of a protrusible copulatory organ which is generally withdrawn within the body cavity except for copulation (Pennak 1989). The female genital pore is usually located at the base of the neck, near the pulmonary aperture or at the edge of the mantle cavity.

Life histories of freshwater gastropods range from annual adults that reproduce once in the spring and die (most pulmonates) to perennial adults that live and reproduce for four to five years (most prosobranchs) (Thorp & Covich 2009). Most freshwater gastropods are oviparous, but some groups, such as the viviparids, are ovoviviparous: the young develop within the female body cavity and are released into the environments as well-developed juveniles (Pennak 1989). Snails usually lay their eggs in the spring in gelatinous cases on various substrates such as plants or rocks. However, oviposition may continue throughout the summer till early fall. With only a one-year life cycle, the semelparous pulmonates produce a lot more eggs than the iteroparous prosobranchs, which may reproduce several times within their lifespan. The former lays clutches of hundreds of eggs at a time, whereas some

prosobranchs such as the pleurocerids, lay clutches of only a few eggs. Young snails have the morphological features of an adult when they leave the egg mass.

Bivalve feeding and life history

In contrast, freshwater bivalves are predominantly specialized in filtering phytoplankton, zooplankton, and organic detritus particles from the water column (Howard & Cuffey 2006). This feeding process occurs by drawing in water through the inhalant branchial siphon, which then goes through the mantle cavity, passes through the outer surface of the gills, and finally back out the exhalant anal siphon (Pennak 1989). This water current is generated by the ciliary action of the gills also called the ctenidia (Thorp & Covich 2009). The ctenidia capture and partially sort the particulate matter, pass it on anteriorly by a ventral ciliated food groove toward the labial palps for further sorting and breaking down before reaching the mouth for ingestion. Smaller bivalves (smaller than a few mm in length) such as the sphaeriids, rely more on deposit feeding within the sediment by using either their foot (pedal feeding) or their inhalant siphon. Therefore, nutrient and plankton-rich waters are favourable to bivalves, although muddy waters with high turbidity from suspended mineral particles are unsuitable for this group of mollusks (Pennak 1989).

Not only used for filter feeding, the internal spaces of the ctenidia also serve as gills for respiration, and as brooding sites for developing embryos and larvae (Thorp & Covich 2009). As observed for freshwater gastropods, the two main groups of bivalves, the clams and the mussels, are differentiated by their life histories.

Freshwater clams, such as the sphaeriids, are hermaphrodites (Pennak 1989). Self-fertilization occurs in the reproductive ducts of each individual. During the developing phase in the ctenidia, an adult clam may contain from 1 to 60 young in various stages of development. When released from the gills through the exhalant siphon, the young are fully developed with the morphological features of adults: direct development (Voshell 2002). In freshwater clams, reproduction occurs throughout the year, however, very few young are released in winter.

In general, freshwater mussels, such as the unionids, have separate sexes (Haag & Staton 2003). Sperm is released through the exhalant siphon and drawn into the inhalant siphon of a nearby female mussel. The female mussel may contain from several thousand to more than 3 million embryos at a time (Pennak 1989). Breeding may begin from the first to the 8th year of life, depending on the species. Some are short-term breeders, between April and August, and others, such as the unionids, are long-term breeders: fertilization occurs in midsummer and then glochidia overwinter until the following spring or summer.

Contrary to freshwater clams, mussels go through a more complex development involving a larval stage and a parasitic stage. During the larval stage, the parasitic larvae, called glochidia, are released from the female mussel, scatterer in the water column, and finally sink to the bottom where they remain with their valves opened upward, waiting to infect a passing fish brushing against the bottom (Zimmerman & Neves 2002). During the parasitic stage, the infected fish forms a cyst as the tissue of the fish grows over the glochidia, which undergoes its metamorphosis within days or weeks depending on species and temperature (Thorp & Covich 2009). A microscopic mussel, then, breaks out of the cyst and falls to the bottom, where the juvenile stage starts and the organs begin to develop. This stage

can last for one to 8 years, until the individual reaches sexual maturity (Pennak 1989).

Gastropod habitat

The majority of freshwater pulmonates live in slow current habitats with silty or solid substrata (Harman 1972). In contrast, limpets and prosobranch algivores such as pleurocerids occupy fast current areas where macrophytes and rocky substrata prevail. Due to their vulnerability to hypoxic conditions, prosobranchs are rarely found in ponds, but are quite common in lakes and rivers. In contrast, pulmonates are common in ponds and vegetated areas of lakes because they are able to tolerate greater variations in dissolved oxygen than prosobranchs. In general, algivores are more common in open freshwater areas, and detritivores prefer bodies of water located in wooded areas (Brown 1982). Some freshwater gastropods are substrate-specific (rocks, silt, or sand), while others are more generalists and occupy a variety of substrate types. Swift streams with sand or gravel bottoms, and wave-swept beaches are poor habitats for gastropods, which are found in low abundance (Pennak 1989).

As a general rule, larger bodies of water tend to have a greater freshwater gastropod diversity than smaller bodies of water due in part to the greater variety of sub-habitats found in the former (Bronmark 1985). The majority of freshwater gastropods occur in shallow waters, less than 3m deep (Pennak 1989). This is mainly due to the associated abundance of food in those areas. Therefore, deeper areas will support lower gastropod abundance than well-illuminated shallow waters favourable to primary producers. With declining temperatures in the fall, individuals migrate towards deeper waters in lakes to hibernate in the mud and debris

on the bottom for the winter, and then go back to the littoral zone in the spring (Thorp & Covich 2009).

Bivalve habitat

In general, freshwater bivalves bury themselves partially or wholly in sediment such as sand, mud, or gravel at the bottom of rivers and lakes (Thorp & Covich 2009). The highest biomass of mussels are found in lotic systems, with a few species occasionally found in wetlands, ponds, or lakes. Freshwater clams are typically found in the same type of habitat as mussels, but they are also adapted to living in temporary ponds, small creeks, and spring brooks. During times of drought, clams burrow deep into the substrate (Pennak 1989).

Freshwater mussels occupy a wide variety of substrate types, usually free of rooted vegetation: mixed mud, sand, gravel, but are rare in areas of bedrock, shifting sand, or deep silt (Thorp & Covich 2009). More generalist in their occurrence, freshwater clams are found on all types of bottoms except clay and rock (Pennak 1989). In contrast with mussels, clams are common in areas with abundant aquatic vegetation (Thorp & Covich 2009). Bare rock bottoms, shifting sands and muds (with high turbidity) are unsuitable for bivalves (Pennak 1989).

Just like freshwater gastropods, freshwater bivalve diversity is greater in larger lakes, than in smaller ones (Pennak 1989). They are also more abundant in shallow nearshore waters less than 2 m deep. Mussels have been found to occur as deep as 7 m in the largest lakes and rivers, whereas clams have been found up to depths of 5 m or more (Thorp & Covich 2009). During the winter, mussels burrow deeper into the bottom for hibernation (Pennak 1989). In

favorable conditions, some mussel beds have more than 50 individuals per square meter. Clams can occur in densities of more than 5000 individuals per square meter under these same conditions.

Environmental factors determining distribution and abundance of molluscs

In addition to general habitat characteristics, a various array of environmental variables seem important in determining the overall distribution and abundance of freshwater molluscs in North America. They are found predominantly in water high in carbonates (Pennak 1989). This is explained by the fact that calcium carbonate is the main building material for the construction of mollusc shells. Greater species diversity and abundance is found in hard water (15 mg/L of bound calcium carbonate versus soft waters (8 mg/L of bound calcium carbonate) (Pennak 1989). A large fraction (45%) of freshwater gastropods are only able to thrive in waters with calcium carbonate concentrations greater than 25 mg/L and 95% of gastropods need levels greater than 3 mg/L (Thorp & Covich 2009). Freshwater clams, however, are better adapted to water low in carbonates with a bound calcium carbonate content of 2 mg/L (Pennak 1989).

Water pH is another factor influencing distribution and abundance of freshwater molluscs, which require alkaline water with a pH above 7.0 (Pennak 1989). Freshwater bivalves are generally found in water with a near-neutral pH, but can withstand a broad range: 5.6-8.3 (Fuller 1974). An acid pH can have a negative impact on their calcareous shells because acids dissolve and erode them, causing considerable mortality (Thorp & Covich

2009). Acid mine drainage is therefore suspected in the extirpation of freshwater bivalves in certain areas of concern (Thorp & Covich 2009). This also explains why freshwater gastropods, for example, are never found in true acid sphagnum bogs (Pennak 1989). However, freshwater clams are adapted to a wider range of conditions and are common in lakes having a pH as low as 6.0 (Pennak 1989).

High dissolved oxygen concentrations are required for most freshwater gastropods (Pennak 1989), which explains their absence in deep oxygen deficient parts of lakes and polluted rivers. However, pulmonate gastropods are able to tolerate greater variations in dissolved oxygen due to their respiratory system (McMahon 1983). On the other hand, freshwater bivalves appear less sensitive to varying oxygen levels. Adult mussels seem relatively insensitive to low oxygen levels (Strayer 2008). They are able to maintain normal metabolism at dissolved oxygen levels as low as 1 mg/L and can tolerate anoxia for several weeks by closing their valves. Juvenile mussel survival, however, may be more limited by inadequate oxygen levels in sediments. With their ability to endure a wide range of dissolved oxygen concentrations, fingernail clams, for example, are able to reside in hypoxic swamps, intermittent streams, and other temporary habitats (Thorp & Covich 2009).

Many other factors such as dispersal ability, temperature, food availability, and invasive species, may limit the distribution of certain freshwater molluscs. Gastropods are mainly dispersed by birds and floods (Pennak 1989). Pulmonate gastropods have a greater dispersal potential because of their adaptation to air breathing (Brown & Johnson 2004). Dispersal can also occur through fish hosts during the parasitic glochidial stage of mussels.

The primary means of dispersal for clams is via birds from one freshwater body to another (Thorp & Covich 2009). Overall, these dispersal mechanisms are passive, making them not entirely reliable for the extension of the distribution of freshwater molluscs.

Few studies have been done on the effects of temperatures on freshwater molluscs. Temperature tolerances seem to vary among freshwater bivalves (Thorp & Covich 2009). However, both high and low temperatures are presumed to be harmful to mussels (Strayer 2008). Moderate warm temperatures therefore seem to be adequate in order to support growth and reproduction.

Food availability limits the distribution of some gastropods. Gastropod diversity is positively related to macrophyte abundance because the latter increases surface area for periphyton colonization (Brown & Lodge 1993). Invasive species such as the zebra mussel can also limit food abundance for native mussels by increasing competition (Strayer 2008). The former also settle and attach themselves to local mussel populations causing large-scale mortality (Thorp & Covich 2009).

Predation and parasites are other natural factors that can control the relative abundance of freshwater molluscs in certain areas. The main freshwater gastropod predators are fishes (suckers, pumpkinseed sunfish, and perch), ducks, shore birds, and other invertebrates such as leeches, crayfish, and beetle larvae (Pennak 1989). Similar to gastropods, freshwater bivalves also have predators, ranging from small invertebrates such as turbellarian flatworm and crayfish, to mammals such as muskrats and raccoon, whose feeding activity is readily

noticeable by the remains of shells along the shoreline of rivers (Diggins & Stewart 2000). Numerous fish such as whitefish, catfishes, suckers, and sunfishes such as pumpkinseeds, are also potential bivalve predators (Thorp & Covich 2009). High predation could lead to a decline in a local mussel population (Thorp & Covich 2009). The parasitic larvae of trematode worms may also impact freshwater gastropod and bivalve population dynamics in certain areas, causing sterility (Sandland et al. 2013; Jokela et al. 1993).

Climate change is also expected to alter the distribution and abundance of freshwater molluscs. Global warming induces droughts and extreme, unpredictable water level variations, which may disrupt the life histories of freshwater gastropods and bivalves (Collas et al. 2014; Gérard et al. 2008; Strayer 2008). Flash floods, caused by heavy precipitation or snowmelts, represent an example of an extreme and unpredictable event, which temporarily disturb mollusc populations and their habitat (Mintsa Nguema et al. 2013).

Anthropogenic factors determining distribution and abundance of molluscs

Anthropogenic factors also play an important role in controlling the distribution and abundance of freshwater molluscs. The construction of impoundments such as dams, have various negative effects on these macroinvertebrates: the former limit distribution and dispersal ability, decrease overall diversity, change rivers from lotic to lentic systems, create hypoxic conditions, lower periphyton abundance (Thorp & Covich 2009), and alter fish communities in the river, therefore reducing the habitat potential of reservoirs to host mussels (Strayer 2008). Dams reduce the ability of host fishes to complete their migration and exert an

influence on the hydrologic regime and longitudinal connectivity of rivers. They reduce the water flow and increased water fluctuations are observed (Vaughn & Taylor 1999). Silt accumulates behind the wall of the reservoir, making this area prone to the sedimentation of toxic metals. Most importantly, dams change rivers from lotic to lentic habitats (Thorp & Covich 2009). After the establishment of a dam, the original mussel fauna may be replaced by silt-tolerant, soft substrate taxa such as anodontines and species of *Leptodea* and *Potamilus* (Blalock & Sickel 1996). Gastropod populations may recover from the dam disturbance further downstream (Satake & Ueno 2012), as was also shown for native mussels. A distance of 20 km below dam impoundments was necessary for a mussel population to recover to pre-dam abundances (Vaughn & Taylor 1999).

Freshwater molluscs are also impacted by a wide variety of diffuse and point source pollution (Thorp & Covich 2009). Due to increasing pollution levels, many species of freshwater gastropods now have ranges that are restricted mainly to headwater streams (Pennak 1989). Freshwater mussels are particularly susceptible to sewage pollution because they are sessile filter feeders, and therefore cannot avoid incoming polluted effluents (Strayer 2008). Sewage effluents consist of a mixture of domestic, municipal, and industrial wastewaters (Bennie 1999). Feminization of the mussel population (Gillis 2012) and impaired immune system functions (Blaise et al. 2002), are potential impacts associated with municipal wastewater effluents. Feminization is a result of endocrine disruption (Gillis 2012). Freshwater mussels are also impacted by runoff from road salt, and elevated chloride concentrations (Gillis 2011). High concentrations of ammonia are toxic and limit the distribution of bivalves (Strayer 2008).

Intensive agricultural activities are another source of pollution to freshwater bodies. Insecticides, herbicides, and fungicides are common types of pesticides that are broadly spread in agricultural fields. These however, contaminate freshwater ecosystems when agricultural runoff occurs. Important concentrations of nutrients and suspended matter are characteristic of agricultural tributaries that drain into rivers (Hudon & Carignan, 2008). This additional source of nutrients to water bodies results in the development of extensive beds of macrophytes and phytoplankton (Vis et al. 2007). Nitrogen limitation is an inevitable consequence of phosphorus fertilizers (Hyenstrand et al. 1998, Schindler et al. 2008), which is shown further downstream by the occurrence of nitrogen-fixing filamentous cyanobacteria such as *Lyngbya wollei* (Tourville Poirier et al. 2010). Characteristic of eutrophication, filamentous green algae provide a food source and refuge for certain freshwater invertebrates (Tessier et al. 2008). Molluscs are potentially impacted by agricultural tributary inputs that alter nutrient concentrations, turbidity, and aquatic vegetation.

Overall, various environmental and anthropogenic factors are crucial in determining the distribution and abundance of freshwater molluscs.

Freshwater molluscs constitute an important macroinvertebrate group in the St. Lawrence River system especially in its fluvial lakes with approximately 9 gastropod families (at least 37 species) and 5 bivalve families (at least 29 species) (Lacoursière et al. 1975; Vincent, 1979; Nalepa & Gauvin 1988; Pinel-Alloul et al. 1996; Desrosiers et al. 2008; Farrell et al. 2010) (See Appendix I). Overall, in the St-Lawrence River, the greatest freshwater mollusc diversity is found within the Unionidae family. In terms of abundance, molluscs constitute a non-negligible macroinvertebrate group in the littoral wetland habitats of Lake

Saint-Pierre (Tall et al. 2008; Tessier et al. 2008). Gastropods, in particular, are found to dominate the fauna associated to macrophytes in this fluvial lake (Tourville Poirier et al. 2010).

Molluscs, however, face various challenges in Lake Saint-Pierre. Several agricultural tributaries drain into this lake altering nutrient concentrations, turbidity, and aquatic vegetation (Hudon & Carignan 2008; Vis et al. 2007). Periodic drying events (Hudon et al. 2005) and exposure to wind fetch are also known to reduce the occurrence of submerged macrophytes in this fluvial lake (Hudon et al. 2005; Hudon et al. 2000). These agricultural tributary inputs and physical perturbations indirectly affect molluscs associated with this aquatic vegetation.

Hypotheses

Our initial hypotheses at the beginning of this study were that stations under the direct influence of enriched agricultural tributaries would support a higher diversity and abundance of molluscs than stations located at increasing distances downstream, that more algivores should be found associated with periphyton and macrophytes, and more filter feeders should be found in waters with high levels of phytoplankton. With our results, however, we noticed that the mollusc community in Lake Saint-Pierre was more influenced by other physical factors such as fetch and elevation.

With this insight, we chose to investigate more closely which characteristics of agricultural tributaries and what other physical variables influence molluscs in Lake Saint-Pierre (St. Lawrence River, Quebec). The main post-hoc hypotheses put forward for our study are that the mollusc community is impacted by the agricultural tributaries and/or by physical variables (desiccation, exposure to waves) through changes in food and habitat. The indicators used were mollusc species composition, diversity, density, and biomass.

Chapitre 2

Multiple stressors affecting the mollusc community in a large fluvial lake

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Abstract

Molluscs are subjected to various anthropogenic and environmental pressures, which consequently determine their distribution, richness, and abundance in freshwater ecosystems. The objectives of this study were to determine the influence of agricultural tributaries and certain physical variables on the mollusk community composition, diversity, and abundance in a fluvial lake of the St. Lawrence River. For this, we sampled molluscs at 14 sites on both shores of Lake Saint-Pierre (3-19 September 2013), and measured physical, chemical, and biological (macrophytes) variables associated with each site. Our results showed a low abundance and richness in mollusc communities and aquatic vegetation at elevated sites (north shore) exposed to periodic emersion conditions and prevailing southwesterly winds. With lower elevations and lower exposure to wind fetch, south shore sites were instead characterized by an abundance of molluscs and submerged macrophyte habitat. Sphaerid clams, however, did not seem to be influenced by these disturbances and were negatively associated with aquatic vegetation. Poor water quality from agricultural tributaries did, however, negatively influence gastropods (total suspended matter and dissolved iron) and unionid mussels (total dissolved phosphorus). With climate change, an increase in extreme and unpredictable disturbance events will likely continue to negatively impact mollusc communities, upon which fish and aquatic birds higher up the trophic food chain depend.

INTRODUCTION

Freshwater molluscs play essential roles in the functioning of aquatic ecosystems. Gastropods provide food for higher consumers such as fish (e.g. suckers, pumpkinseed sunfish, and perch), ducks, shore birds, and other invertebrates such as leeches, crayfish, and beetle larvae (Pennak 1989). Bivalves also are a source of food for predators ranging from small invertebrates such as turbellarian flatworm and crayfish, to mammals such as muskrats and raccoons (Gale 1969; Thorp & Covich 2009).

The majority of freshwater gastropods are herbivores, grazing on periphyton that covers submerged surfaces such as macrophytes or cobble (Pennak 1989). Gastropod densities and species composition tend to be positively associated with macrophyte occurrence (Cyr and Downing 1988; Strayer and Malcom 2007) because submerged aquatic vegetation increases surface area for periphyton colonization (Thorp & Covich 2009). In contrast, bivalves are predominantly filter feeders, specialized in removing suspended microscopic phytoplankton, zooplankton, and organic detritus particles from the water column (Howard & Cuffey 2006).

Molluscs also serve as good bioindicators of water quality (Oehlmann & Schulte-Oehlmann 2002). If a pollutant negatively impacts molluscs, it will most likely have detrimental effects on the entire freshwater ecosystem. Unionid mussels exhibit a marked decline in North America, including in the St. Lawrence River, owing to the introduction of zebra mussels, habitat degradation and poor water quality (Paquet et al. 2005).

A diversified fauna of freshwater molluscs has been reported in the St. Lawrence River system especially in its fluvial lakes with approximately 9 gastropod families (at least 37

species) and 5 bivalve families (at least 29 species) (Lacoursière et al. 1975; Vincent, 1979; Nalepa & Gauvin 1988; Pinel-Alloul et al. 1996; Desrosiers et al. 2008; Farrell et al. 2010). Overall, in the St-Lawrence River, the greatest freshwater mollusc diversity is found within the Unionidae family.

In Lake Saint-Pierre, the largest ($\approx 300 \text{ km}^2$) of the St. Lawrence fluvial lakes, molluscs are one of the most important and varied group of macroinvertebrates (Tall et al. 2008; Tessier et al. 2008) although a decline has been recently observed in some areas (Tourville Poirier et al. 2010). Mollusc populations face a number of challenges in Lake Saint-Pierre. Several agricultural tributaries drain into this lake altering nutrient concentrations, turbidity, and aquatic vegetation (Hudon & Carignan 2008; Vis et al. 2007). A lower abundance of molluscs was observed in sediment and emergent vegetation habitats of Lake Saint-Pierre in sites situated in the plume of tributaries than in reference sites (Tall et al. 2008).

Lake Saint-Pierre is also subject to important interannual and seasonal water level fluctuations (Hudon et al. 2005; Hudon 1997). Low water levels, which expose shallow areas, and make molluscs directly vulnerable to dessication (Collas et al. 2014). Moreover, drying events reduce the occurrence of submerged macrophytes the following years (Hudon et al. 2005) indirectly affecting molluscs associated with this aquatic vegetation. Due to the large size (about 30 km along its longest axis) and SW-NE-orientation of Lake Saint-Pierre, the north shore of the lake is particularly exposed to waves generated by the south-west winds that predominate during summer months. Areas exposed to wind and waves (large fetch) are known to support lower biomasses of submerged macrophytes (Hudon et al. 2000) and

freshwater molluscs (Burton et al. 2004) than more protected areas.

The objective of this study was to explore the variables affecting the mollusc communities of Lake Saint-Pierre in view of their importance in the trophic chain and of perceived threats to their stability. We addressed the effects of the tributaries by sampling at different distances from their inputs. We chose sites on both the north (exposed) and south (protected) shores of the lake to evaluate the influence of winds and waves. Finally, the unusually low water levels registered the year preceding our sampling, allowed us to identify possible outcomes of periodic emersion of our sites on mollusc species composition, diversity, density, and biomass.

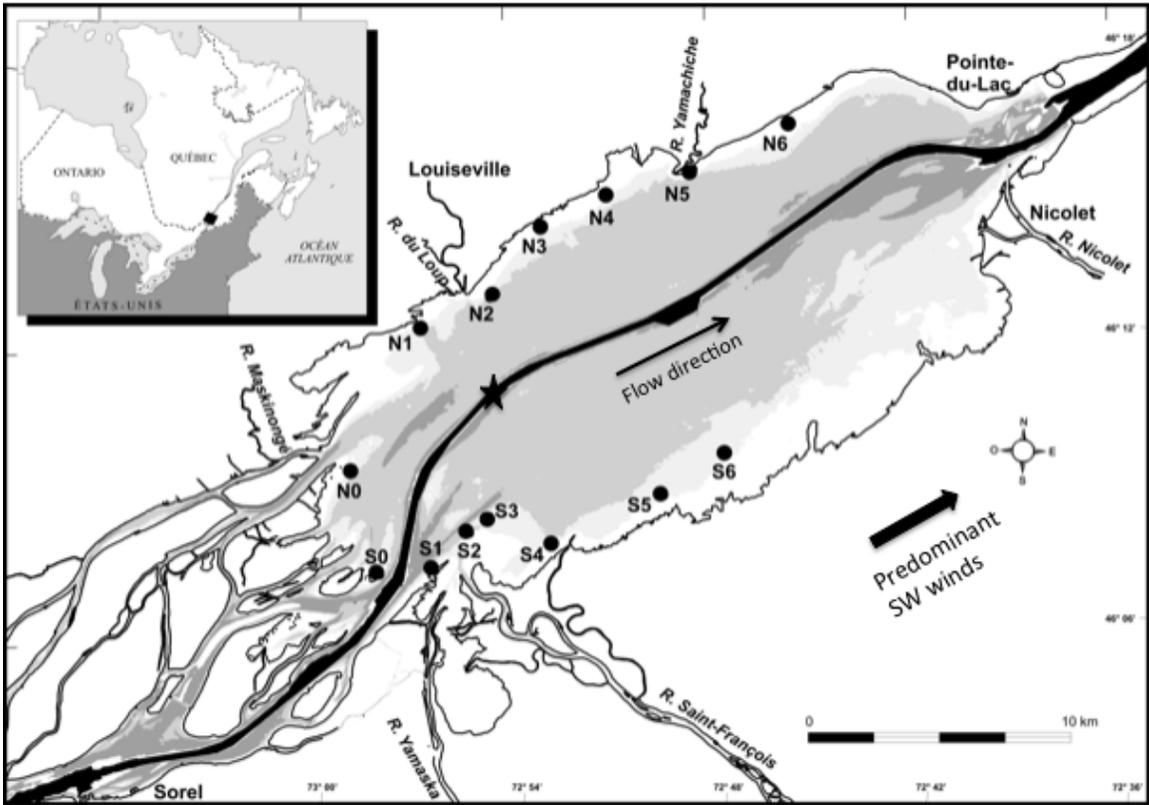
The main hypotheses for this study were that the mollusc assemblages are impacted by the agricultural tributaries and/or by physical variables (desiccation, exposure to waves) through changes in food and habitat. We supposed that gastropods and bivalves could be differently affected by these variables in view of their different food sources, dependence on macrophytes, and capacity to withstand emersion.

METHODS

Study site

Lake Saint-Pierre (46.20 N, 72.85 W), a fluvial lake of the St. Lawrence River, is located 85 km downstream of the city of Montreal, Quebec, Canada. This widening of the river is relatively shallow (mean depth ~3 m) and slow-flowing (<0.5 m/s), with the exception of a man-made central navigation channel (depth >11 m) in which a significant portion of the flow (0.5–1 m/s) is now concentrated (Hudon & Carignan 2008) (Figure 1).

Figure 1. Sampling sites in Lake Saint-Pierre (St. Lawrence River, Quebec). 14 sites with 7 sites on each shore (north and south). The major tributaries are the Maskinongé, Du Loup, and Yamachiche rivers, on the north shore, and Yamaska and Saint-François rivers on the south shore. The bathymetry, predominant SW winds, flow direction, navigation channel, and gauging station are indicated.



Several agricultural tributaries drain the north (Du Loup and Yamachiche rivers) and south (Yamaska/Saint-Francois rivers) portions of the Lake Saint-Pierre watershed (Table I). These rivers drain croplands, dairy farms, and woodlands (Tall et al. 2008). Yamaska River is one of the most agriculturally polluted rivers in the Quebec province (St-Onge 1999; Hudon & Carignan 2008). The north shore differs from the south shore due to an increased exposure to the prevailing South-West wind, and having multiple agricultural tributary inputs (Table I; Figure 1).

Important annual and seasonal water level fluctuations occur in Lake Saint-Pierre, with generally higher levels during the spring (April-June) and lower levels during the summer (July-September) (Figure 2). Interannual differences are also important: in 2012, summer water levels reached extreme low conditions between July and October (< 3.3 m IGLD85), whereas minimum levels in summer 2013 remained near the long-term average (> 3.5 m IGLD85) (Figure 2). Therefore, large areas of shallow-water riparian areas submerged during the summer of 2013 had been emerged intermittently or continuously for a period of several weeks over the summer of 2012.

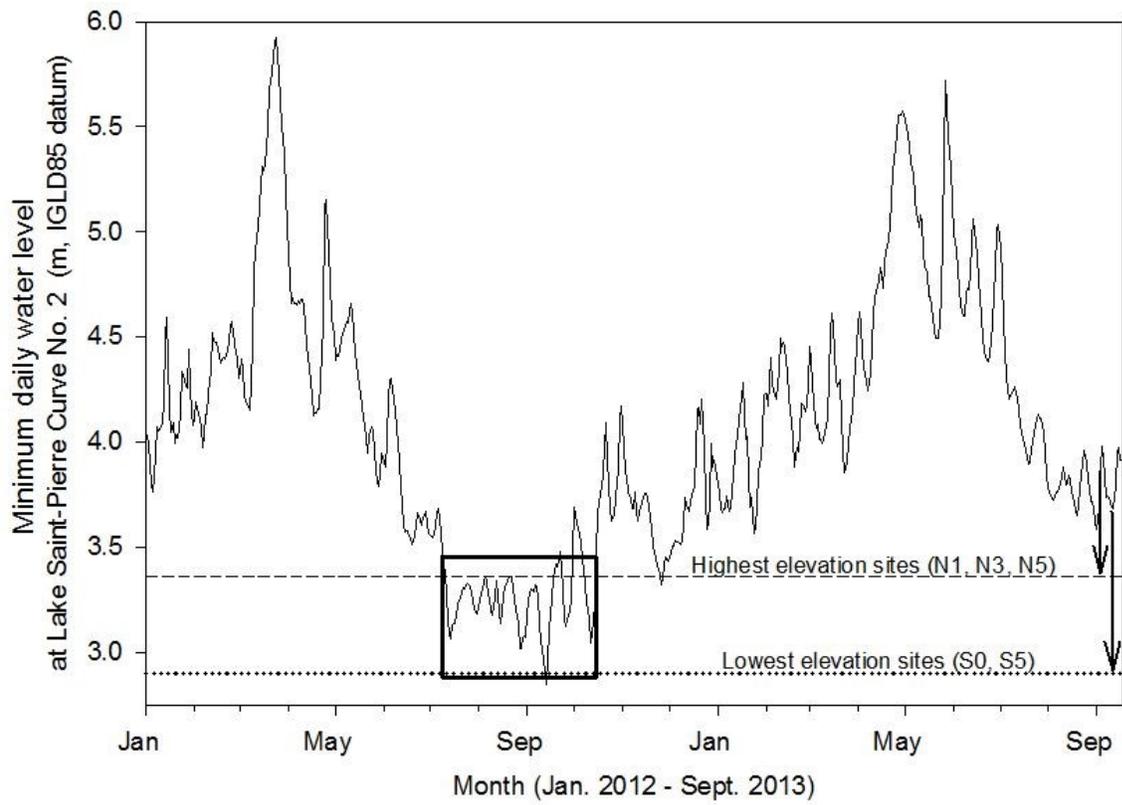
Sampling sites

Fourteen sites were sampled in total comprising two reference sites (Figure 1). On the north shore, the reference site N0 was located across the pleasure boating channel, away from the influence of small local tributaries (Bayonne, Chicot, Maskinongé rivers) and the wastewater inflow of the city of Berthier. On the south shore, the reference site S0 was

Table 1. Comparison of land use, physical and chemical characteristics of Lake Saint-Pierre tributaries * mean summer variables (May-September). Mean annual discharge 2000-2005 (min-max) and mean annual values (s.d., N) are indicated for water quality variables. ¹ Hudon & Carignan, 2008, ² Robitaille, 2005, ³ MDELCC, 2015, ⁴ OBV Yamaska, 2012, ⁵ COGESAF, 2014, ⁶ Statistics Canada, 2011, ⁷ US Population Census, 2010, ⁸ MAPAQ, 2004, ⁹ OBVRLY, 2014.

	North Shore		South Shore	
	Du Loup River	Yamachiche River	Yamaska River	St-François River
Surface area (km ²)	1 589 ²	266 ⁹	4 784 ⁴	10 230 ⁵
Agricultural surface area (%)	8.5 ⁸	14.2 ⁶	52.4 ⁴	10.8 ⁶
Population (individuals)	15 774 ²	6 983 ⁶	250 000 ⁴	501 511 ^{6,7}
Mean annual discharge (m ³ /s)	n/a	n/a	86 (2-1278) ¹	168 (8-1452) ¹
Conductivity (µS/cm)	65.9 (21.3, 18) ^{*3}	161.2 (44.3, 18) ^{*3}	360 (72.8, 16) ^{*3}	195.6 (56.1, 18) ^{*3}
Suspended particulate matter (mg/L)	11.4 (5.2) ^{*3}	52.2 (57.4, 18) ^{*3}	58.1 (46.5, 16) ^{*3}	30.1 (70.6, 18) ^{*3}
Dissolved organic carbon (mg/L)	4.4 (0.8, 18) ^{*3}	4.7 (1.1, 18) ^{*3}	6.3 (1.2, 16) ^{*3}	6.8 (1.2, 18) ^{*3}
Total phosphorus (µg P/L)	28 (8, 18) ^{*3}	105 (61, 18) ^{*3}	98 (49, 16) ^{*3}	44 (70, 18) ^{*3}
Total nitrate (µg N/L)	380 (150, 18) ^{*3}	1340 (330, 18) ^{*3}	2070 (1330, 16) ^{*3}	690 (230, 18) ^{*3}
Nitrite/Nitrate (µg N/L)	170 (80, 18) ^{*3}	970 (210, 18) ^{*3}	1530 (1280, 16) ^{*3}	340 (160, 18) ^{*3}
Ammonium (µg N/L)	40 (40, 18) ^{*3}	180 (200, 18) ^{*3}	40 (30, 16) ^{*3}	30 (10, 18) ^{*3}
Chlorophyll-a (µg/L)	1.36 (0.65, 18) ^{*3}	2.29 (1.63, 18) ^{*3}	20.9 (20.1, 16) ^{*3}	4.9 (3.6, 18) ^{*3}

Figure 2. Variations of minimum daily water levels (m, IGLD85 datum) from January 2012 to September 2013 at Lake Saint-Pierre (Curve no. 2 gauging stations). The range of elevation of sampling sites is indicated relative to water level fluctuations, contrasting sites of highest (slashed line) and lowest (dotted line) elevation. Vertical arrows indicate water depth at the time of sampling (Sept. 2013). The period of July-October 2012, during which sites were periodically emerged is identified (box).



situated across the navigation channel, far from the plume of the tributaries (Yamaska, Saint-François, and Richelieu rivers) and of the wastewater outflow of the city of Sorel. Two sites (N2, N5) on the north shore and three sites (S1, S2, S3) on the south shore were located proximately downstream (< 3 km) of a tributary mouth. The other 8 sites, situated at increasing distances (3 to 13 km) downstream from the inflow of tributaries, were considered to represent a gradient of decreasing exposure to tributaries.

Sampling sites also differed according to their elevation with respect to sea level, which largely determined the emersion-submersion regime to which they had been subjected over the previous year. Individual site elevation was calculated by subtracting the water depth measured at each site at the time of sampling from the corresponding hourly water level value (meters, IGLD85 datum) for Lake Saint-Pierre (Gauging station no. 15975, Courbe no 2, Department of Fisheries and Oceans, DFO 2014) (<http://www.charts.gc.ca/index-eng.asp>). The sequence of water depth and the duration of dry episodes experienced at each site was then reconstructed from the hourly time series of water level variations between January 1st 2012 and the sampling date in September 2013.

Field sampling

Sampling took place over a period of 2 weeks in late summer 2013 (3-19 September). Sites were located at pre-determined distances along the north and south shore and were selected to correspond to a depth range of 70-100 cm at the time of sampling. Position of each site was determined using a DGPS (Garmin GPSMap 76C and GBR21 receiver coupled to a Canadian Coast Guard differential beacon). Since sampling was carried out by operators on

foot and water level fluctuated from day to day by as much as 36 cm, the elevation of sites that were accessible for sampling ranged from 2.9 to 3.36 m asl.

At each sampling site, we carried out measurements of physical and chemical water quality, submerged plant biomass, and sediment granulometry.

Water quality measurements

At each site, turbidity (NTU), conductivity ($\mu\text{S}/\text{cm}$), temperature ($^{\circ}\text{C}$), dissolved oxygen concentration (mg/L) and percent saturation (%), pH were measured with a multiprobe (YSI 600 XLM, YSI, Yellow Springs, Ohio). Current velocity (SonTek, FlowTracker Handheld-ADV Model P300, San Diego, USA), water depth (cm), and underwater light penetration (LI-COR LI-190SA air and underwater LI-193SA spherical sensors, LI-COR Biosciences, Lincoln, Nebraska) were also obtained. Light extinction coefficient (k) was calculated using the slope of the ln-transformed values of light penetration at increasing depth (I_z), divided by surface light intensity (I_0). Water samples were collected below the water surface and were kept in a cooler until brought back to the laboratory for processing. Unfiltered subsamples were analyzed for total suspended matter (TSM), total phosphorus (TP), and total nitrogen (TN). Filtered subsamples (Whatman GF/C, General Electric Healthcare Life Sciences, Piscataway, New Jersey) were analyzed for total dissolved phosphorus (TDP), total dissolved nitrogen (TDN), nitrite/nitrate (NO_2^- - NO_3^-), ammonium (NH_4^+), dissolved organic carbon (DOC), dissolved calcium, dissolved iron, phytoplankton chlorophyll-a, and color (Pt/Co method) using standard protocols (Environment Canada 2005).

Habitat characteristics

The biomass of aquatic vegetation was determined using a 35 cm wide double-sided rake (Yin et al. 2000), which was dragged over a length of 1 m. At each site, five replicate rake samples were collected, which were averaged to estimate mean biomass per site. The vegetation collected with the rake was brought back to the laboratory, where it was rinsed to remove sediments and debris, identified, and weighed wet. Vegetation was subsequently dried (50°C) and weighed (to the nearest 0.1 mg). Filamentous green algae and benthic cyanobacteria were sorted from macrophytes and separately weighed. Superficial sediments were sampled at every station with an Ekman dredge in order to determine the granulometry (Environment Canada 2005).

Mollusc sampling

Molluscs were sampled using a triangular dip net (500 µm mesh) with a 465 cm² opening (30.5 cm wide base x 30.5 cm height). Molluscs found in the water column were first sampled by sweeping the dip-net up and down through the water column over a distance of 4 m. Molluscs closely associated to the bottom were then sampled by shuffling the dipnet through the sediment and submerged vegetation (macrophytes, filamentous cyanobacteria) over the same area. Three to five replicate samples of molluscs were collected within the water column and in the surficial sediment at every site. Only three replicates were collected at sites with great mollusc abundance (S1, S3, S4, S5, S6, N0).

Laboratory sorting, identification and measurements

Molluscs associated with macrophytes and sediments were sorted with the naked eye and under the dissecting microscope at the 6X magnification. We identified all individuals to the farthest possible taxonomic level following Clarke (1981) and Peckarsky et al. (1990) (for more details on sorting and identification methods, consult Appendix II). The density of each mollusc family was averaged per site (mean \pm s.d.) and converted to units/ m² considering a sampled surface area of 4 x 0.3 m (net width) for each replicate sample.

For all individuals, we measured a specific body dimension (mm): shell height, shell width, shell length or aperture width. Large molluscs (Unionidae, Dreissenidae, and Viviparidae families) were measured with a digital vernier (\pm 0.5 mm precision) whereas small ones (including unionid mussels < 7mm in length), were measured using an image analyser system connected to a dissecting microscope (Image Pro-Plus 7.0; Media Cybernetics Inc., Bethesda Md). Body dimensions (mm) were converted to shell-free dry mass using previously published conversion equations (for more details on measurement and biomass calculation methods, consult Appendices II and III) (Méthot et al. 2012; Ozersky et al. 2012; Benke et al. 1999; Balfour & Smock 1995; Mackie 1991; Cameron et al. 1979; Greig, unpublished data).

Statistical analyses

A principal component analysis (PCA) based on water physical and chemical data was used to identify variation among sites and relationships between variables. Redundancy analyses (RDA) were performed to relate mollusc community composition with environmental characteristics (physical, chemical, and habitat). To minimize the effect of absent taxa, data

was normalized prior to analysis using the Hellinger transformation (Legendre & Gallagher 2001). These multivariate analyses were performed using using CANOCO 4.5 for Windows (ter Braak and Smilauer 2002).

The *Shannon Diversity Index* was calculated with the following equation: $H' = -\sum (p * \ln p)$, where p is the proportion (n/N) of individuals of one particular species found (n) divided by the total number of individuals found (N). ln is the natural log, and Σ is the sum of the calculations (Shannon & Weaver 1948). The *Pielou Evenness Index* was calculated with the following equation: $J = H' / \ln(s)$, where H' is the *Shannon Diversity Index* and s is the number of species (Pielou 1966).

Relationships of univariate variables (mollusc density and biomass, macrophyte biomass, and diversity indices) with environmental variables were analyzed using Forward Stepwise multiple regression (Statistix, Analytical Software, Tallahassee, Florida). When necessary to achieve normality, variables were log transformed prior to analyses.

RESULTS

Physical, chemical and habitat characteristics

Sampling sites were experiencing widely different wave exposure as estimated by fetch along the prevailing south-west winds. Fetch from the south-westerly winds was < 3 km for sites located along the protected south shore but increased progressively towards the east for sites located along the north shore, reaching a maximum value of 24 km at the easternmost site (N6) (Table II; Appendix IV). Water current velocity at the time of sampling ranged from 2.2

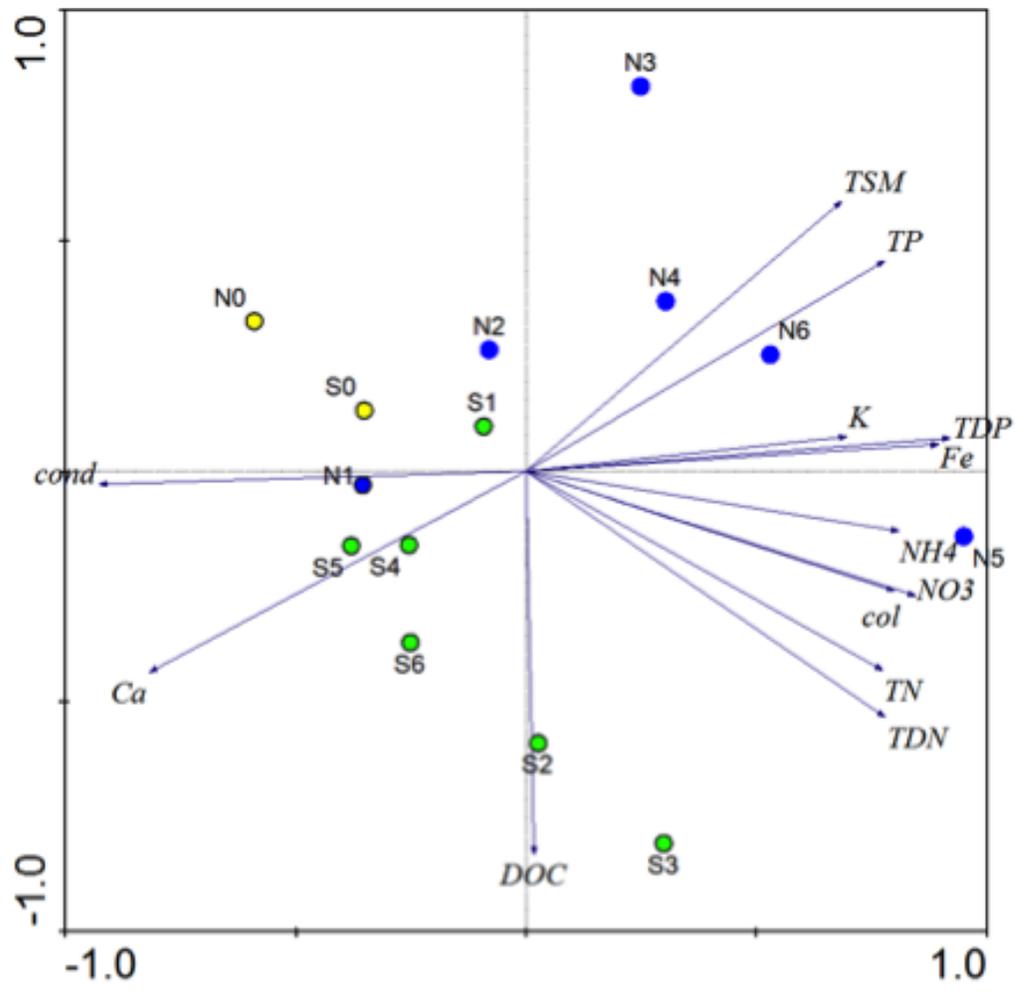
to 18.6 cm/s. Site elevation varied from 3.36 (N3) to 2.90 (S0) m, resulting in sharp differences in emersion periods during the unusually low water levels which occurred in the year preceding our 2013 sampling. Sites located at the highest elevations (N1, N3, N5) endured periodic emersion over a cumulative period of > 50 days during the 3 months from mid July to mid September 2012 (Figure 2; Table II). In contrast, sites located at the lowest elevations (S0, S2, S3, S5) were emerged sporadically, a few hours per day, for cumulative periods < 3 days over the same time frame (Figure 2; Table II). All sites had similar sediment composition that were characterized by a high percentage of sand (>83% for all sites except S3), and with more than 9% silt at three sites (N2, N4, and S3).

Water physical and chemical variables also differed among sites situated on the two shores and at different distances from the agricultural tributary input (for more details, consult Appendix V). In a principal component analysis (PCA) based on chemical water variables, axis I explain 61% of the variance among sites. Axis I allowed to contrast sites that were subjected to nutrient rich waters (all forms of nitrogen, phosphorus, dissolved iron, water color, and TSM) originating from tributaries (right side of the axis) with sites that were more influenced by waters from the Great Lakes, characterized by high conductivity and calcium concentrations (left side of axis I) (Figure 3). Axis II represented a gradient in dissolved organic carbon (DOC), in opposition with a small contribution from total suspended matter (TSM) and total phosphorus (TP) (Figure 3). The PCA highlighted differences between the sites on the north shore of Lake Saint-Pierre (mainly on the upper-right quadrant) associated with high nutrients and low DOC and those on the south shore (mainly on the lower left

Table II. Comparison of the morphometry of each sampling site.

	North Shore						South Shore							
	N0	N1	N2	N3	N4	N5	N6	S0	S1	S2	S3	S4	S5	S6
Latitude N	46.16	46.21	46.22	46.24	46.25	46.26	46.27	46.12	46.12	46.14	46.14	46.13	46.15	46.16
Longitude W	72.98	72.94	72.91	72.88	72.85	72.81	72.76	72.97	72.94	72.92	72.91	72.88	72.83	72.79
Cumulative distance downstream (km)	-2	8.5	11.6	14.5	17.3	21.2	25.3	-2.0	-1.5	1.6	2.6	5.4	9.9	12.8
Distance downstream from nearest tributary (km)	-2	8.5	1.4	4.3	7.3	1	5.1	-2	2.7	1.6	2.6	5.4	9.9	12.8
Fetch SW (km)	2.3	5	8.5	10	13.7	19.6	24	3	0.5	1.6	2	1.5	2.9	6
Elevation (m, asl)	3.16	3.35	3.31	3.36	3.22	3.35	3.29	2.90	3.10	3.03	3.00	3.17	2.94	3.17
Number of days out of water in summer 2012	11.5	53.3	42	56.5	21.2	53.3	37	0	5.1	2.2	1.4	12.5	0.4	12.5

Figure 3. Principal Component Analysis of chemical variables measured at each station (Blue dots indicate north shore sites, green dots indicate south shore sites, and yellow dots indicate control sites).



quadrants) associated with lesser concentrations of nutrients, TSM, and high DOC (Figure 3). Control sites (N0 and S0) were grouped together and associated with high conductivity, indicative of waters from the main river stem.

The differences between sites on the two shores highlighted by the PCA and contrasting exposure of the north and south shores to the prevailing SW winds (Table II) justified our subsequent characterization of sites for each shore separately. On the north shore, total suspended matter (TSM), total dissolved phosphorus (TDP), nitrite/nitrate (NO₂/NO₃), and dissolved organic carbon (DOC) concentrations tended to increase with cumulative distance from the reference site with spikes following the inflow of agricultural tributaries such as the one observed for NO₂/NO₃ (1.21 mg N/L) after the Yamachiche River (N5) (Figure 4a). In contrast, along the south shore, these variables decreased steadily downstream after the initial rise in concentration following the inflow of the Yamaska and Saint-François rivers (Figure 4b). With the exception of DOC concentration that was highest along the south shore, all the other enrichment descriptors were more elevated at north shore sites.

Aquatic Vegetation

Macrophytes dominated by *Vallisneria americana*, *Potamogeton richarsonii*, and *Heteranthera dubia* reached a biomass > than 10 g dry mass/m² at three sites on the south shore (S2, S3, S5) whereas the north shore was almost devoid of submerged vegetation (Figure 5a). Metaphytic filamentous green algae were rarely present on either shore, reaching a sizeable amount (> 0.1 g dry mass/m²) only at site N2 and S3. The benthic cyanobacterium *Lyngbya wollei* was abundant (41 g dry mass/m²) at site S1, occurred in trace amounts (< 1g dry mass/m²) at S3 and S5, and was absent elsewhere. Phytoplankton concentrations (as

Figure 4. Water chemistry (TP, nitrates/nitrites, DOC, dissolved iron, TSM) characteristics at sampling stations located at increasing distance downstream along the north (a) and south (b) shores of Lake Saint-Pierre (dotted lines indicate agricultural tributary inputs).

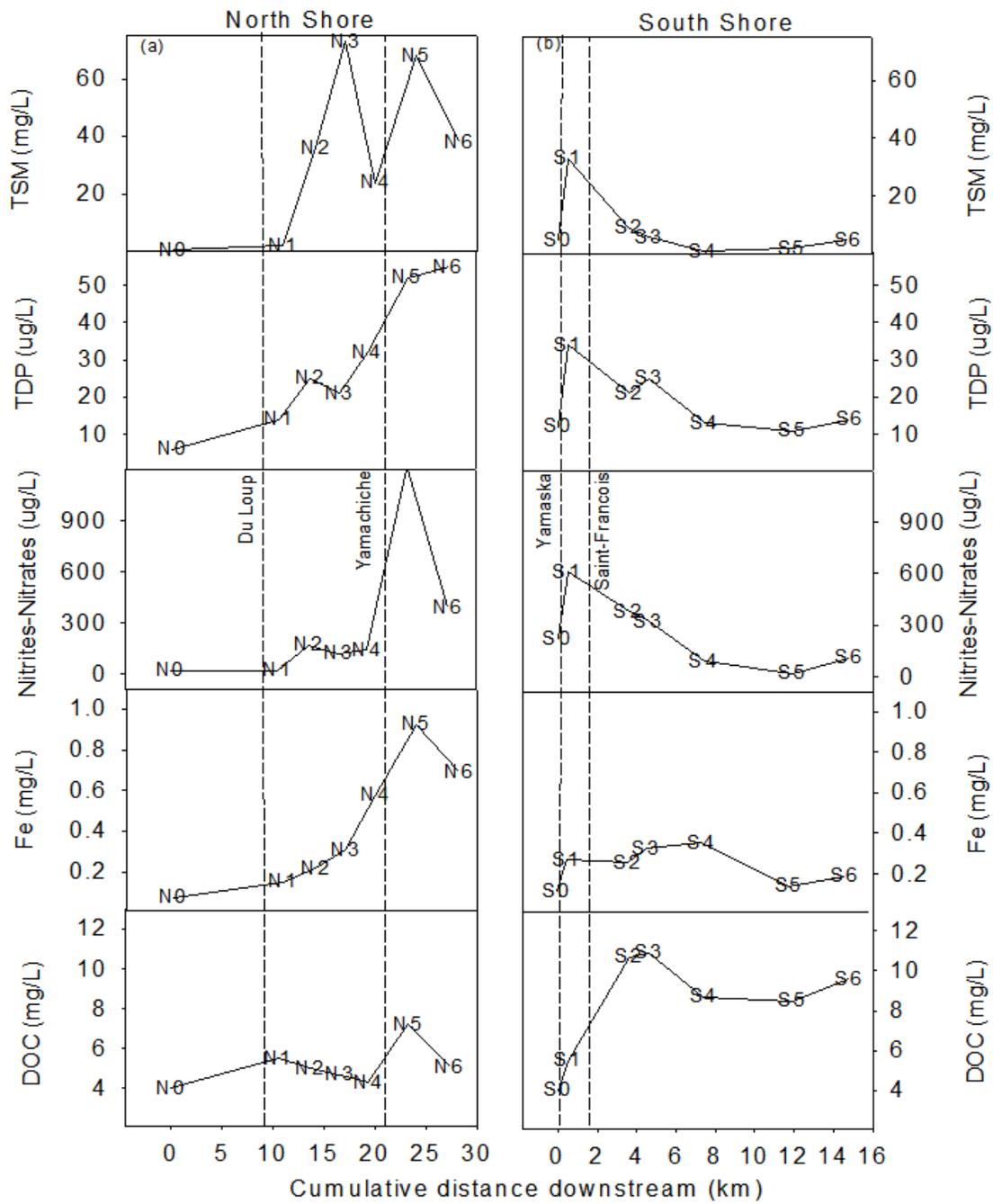
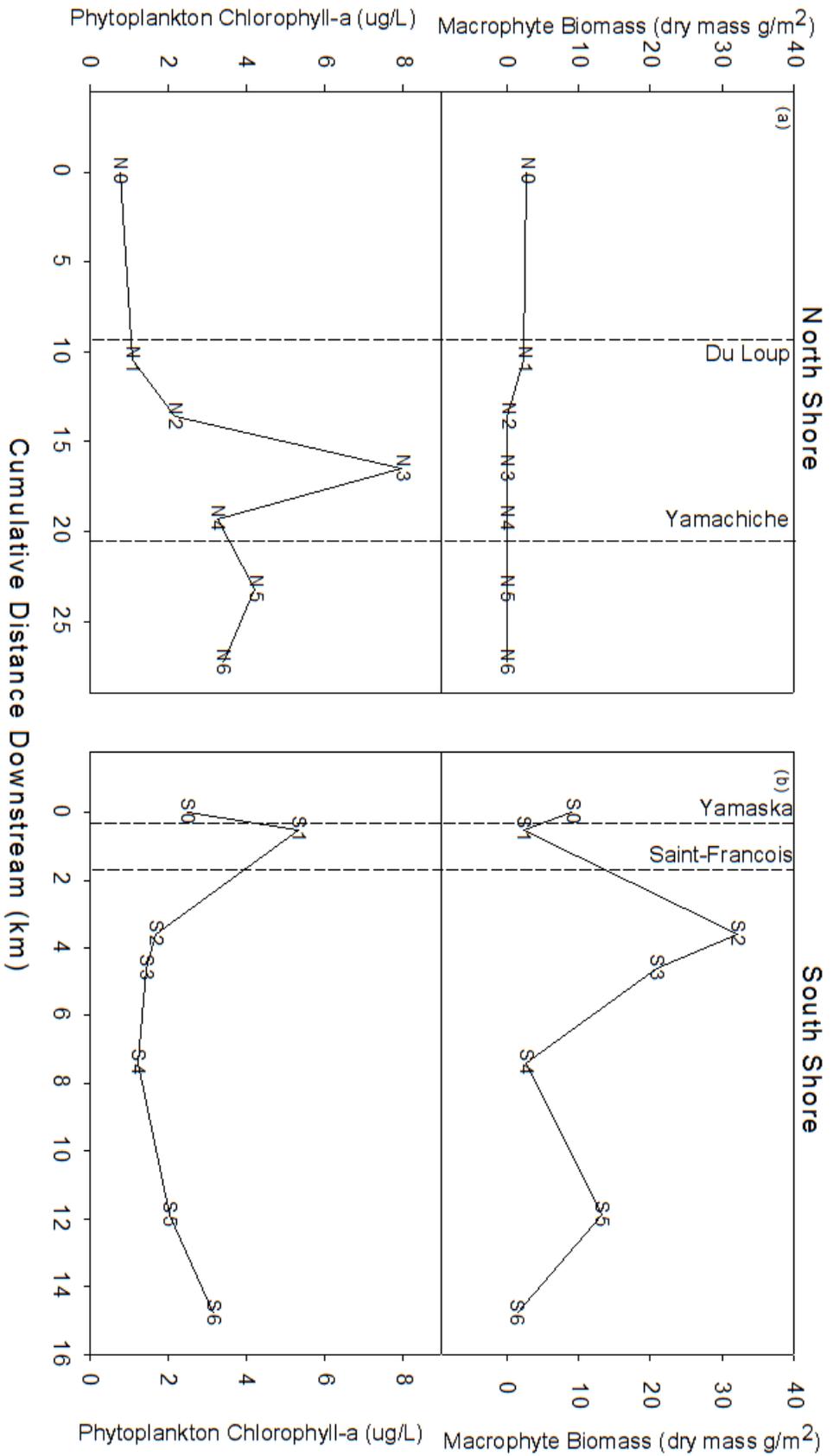


Figure 5. Biomass of submerged macrophytes (a) (upper), and phytoplankton chlorophyll-a (b) (lower) for stations located at increasing distance along the north and south shores of Lake Saint-Pierre (dotted lines indicate agricultural tributary inputs).



chlorophyll-a) ranged widely from 0.8 (site N0) to 8.0 µg/L (site N3). Concentrations tended to be higher along the north shore than the south shore and increased downstream of the tributary inputs (Figure 5b) mirroring the trends previously described for nutrients and TSM (Figure 4).

Mollusc taxonomic and size composition

Seventeen gastropod and 8 bivalve species were observed throughout our study (Table III). The most frequently observed gastropods (70% of sites) were *Amnicola limosa* and *Probythinella lacustris* (Hydrobiidae), *Ferrissia* spp. (Ancylidae), *Physa gyrina* (Physidae), and *Gyraulus parvus* (Planorbidae). Among bivalves, sphaeriidae clams were very frequent with *Pisidium* spp. observed at all sites and *Sphaerium* spp. at 70% of all sites. The most widespread unionid mussels were *Elliptio complanata* and *Lampsilis radiata*, which were observed at 74% and 61% of sites, respectively). The other unionidae, *Lampsilis cardium*, *Leptodea fragilis*, and *Strophitus undulatus*, were observed only at the south shore site S3. The invasive zebra mussel (*Dreissena polymorpha*) was collected everywhere on the south shore but was found on the north shore only at the reference site N0.

The molluscs observed in our study spanned over a large size range. Gastropods ranged between 0.8 µg and 317 mg shell-free dry mass (Table III; Appendix XIX). The Ancylidae were prevalent in the smallest size class (<0.01 mg dry mass), the Hydrobiidae dominated the middle size classes (0.01-10 mg dry mass), whereas the Viviparidae were the only gastropod family found in the largest (10-1000 mg dry mass) size class. Sphaerid clams were the smallest bivalves ranging in size between 6 µg and 5.5 mg shell-free dry mass with numerous juveniles (< 0.01 mg dry mass) (See Appendix XX). Unionid mussels were the largest

Table III. Mollusc species sampled in Lake Saint-Pierre (columns with abbreviations used for RDA, mean individual size, size range (min-max), abundance range (min-max), and number of sites found; *after verification *Valvata bicarinata* are actually *Valvata tricarinata*).

Family	Species	RDA	Mean Size (mg)	Size Range (mg)	Abundance Range (ind/m ²)	Number of Sites Found (N/14)		
Prosobranch Gastropods	Bithyniidae							
		<i>Bithynia tentaculata</i> (Linnaeus)	Bite	4.0	0.3-15.0	0.2-4.7	4	
	Hydrobiidae							
			<i>Amnicola limosa</i> (Say)	Amlu	0.8	0.02-3.1	0.2-65	13
			<i>Birgella subglobosa</i> (Say)	Bisu	1.8	0.9-3.8	0.3-0.8	2
		<i>Probythinella lacustris</i> (Baker)	Pr1a	0.8	0.05-2.0	0.5-28.3	10	
	Pleuroceridae							
			<i>Goniobasis livescens</i> (Menke)	Goli	18.1	9.2-30.8	0.3-3.1	5
		<i>Pleurocera acuta</i> (Rafinesque)	Plac	10.9	0.3-49.4	0.2-4.2	8	
	Valvatidae							
			<i>Valvata bicarinata</i> (Lea)*	Vabi	0.07	0.03-0.1	0.2-1.1	5
			<i>Valvata piscinalis</i> (Muller)	Vapi	4.1	4.1	0.3	1
			<i>Valvata sincera</i> (Say)	Vasi	0.03	0.001-0.2	0.3-4.7	7
		<i>Valvata tricarinata</i> (Say)	Vatr	0.6	0.005-1.3	0.2-1.7	4	
Viviparidae								
		<i>Campeloma decisum</i> (Say)	Cade	129.6	96.8-150.2	0.3	3	
		<i>Viviparus georgianus</i> (Lea)	Vige	156.4	8.6-317.4	0.3-10	5	
Pulmonate Gastropods	Ancylidae							
		<i>Ferrisia</i> (Walker)	Ferr	0.02	0.0008-0.2	0.2-240	12	
	Lymnaeidae							
			<i>Pseudosuccinea columella</i> (Say)	PSCO	5.1	0.07-47.7	0.2-2.8	5
	Physidae							
	<i>Physa gyrina</i> (Say)	Phgy	0.6	0.003-17.9	0.2-16.1	11		
Planorbidae								
		<i>Gyraulus parvus</i> (Say)	Gypa	0.2	0.0009-0.9	0.2-52.2	11	
	<i>Helisoma trivolvis</i> (Say)	Hetr	2.3	0.005-18.1	0.2-4.4	3		

Bivalves									
Dreissenidae	Sphaeriidae	<i>Dreissena polymorpha</i> (Pallas)	Drpo	36.3	0.02-169.1	0.6-7.2	5		
		<i>Pisidium</i> (Pfeiffer)	Pisi	0.09	0.01-5.5	2.5-484.8	14		
Unionidae		<i>Sphaerium</i> (Scopoli)	Spae	0.9	0.01-5.5	0.2-6.5	10		
		<i>Elliptio complanata</i> (Lightfoot)	Elli	1310.9	0.001-7133.8	1.0-16.9	10		
		<i>Lampsilis radiata</i> (Gmelin)	Lamp	2438.6	284.54-5144.5	0.5-9.7	9		
		<i>Lampsilis cardium</i> (Rafinesque)	Lamp	5784.5	5784.5	0.3	1		
		<i>Leptodea fragilis</i> (Rafinesque)	Lept	3626.1	3626.1	0.3	1		
		<i>Strophitus undulatus</i> (Say)	Stro	222.6	222.6	0.3	1		

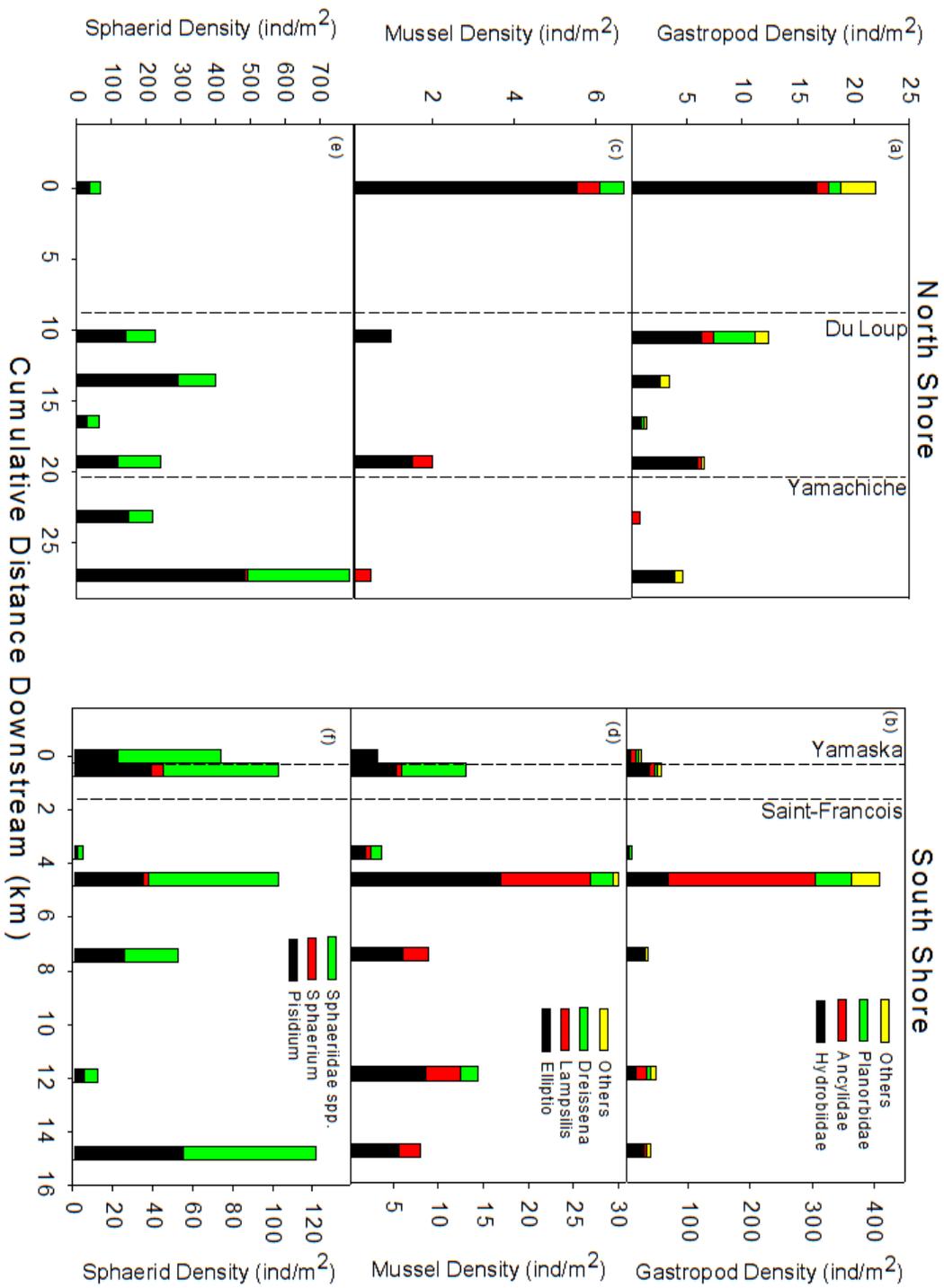
molluscs reaching 7 g shell-free dry mass whereas Zebra mussels were found in the 10-1000 mg dry mass size class.

Mollusc density, biomass and diversity

Gastropod densities were rather low at north shore sites, showing a steady decrease from the reference site (N0; 22 ind/m²) to values < 5 ind/m² towards downstream sites (Figure 6a). Hydrobiidae were dominant representing overall 71% of gastropod density. Along the south shore, gastropod densities were considerably higher than on the north shore, averaging 37 ind/m² even excluding the extreme high value (408 ind/m²) found at S3 (Figure 6b). Ancyliidae were the dominant family (46% of gastropod density) followed by Hydrobiidae (29%), and Planorbidae (12%). When considering Unionidae mussels, the differences in densities between the two shores were even more evident than for gastropods. Unionidae densities never exceeded 2 ind/m² along the north shore and were altogether absent at three sites (Figure 6c). In contrast, south shore sites supported densities around 8 ind/m² with a sharp peak (27 ind/ m²) at site S3 (Figure 6d). *Elliptio complanata* was everywhere the dominant species. *Lampsilis radiata* was more frequently recorded on the south shore (25%) than on the north shore (15%). A contrasting pattern was observed for sphaeriidae that were most abundant in the north shore (maximum density of 785 ind/m² at site N6 (Figure 6e), whereas densities rarely reached 100 ind/m² at south shore sites (Figure 6f). *Pisidium* spp. was the most abundant sphaerid taxon at all sites. *Sphaerium* spp. was relatively more abundant on the south shore (2%) than on the north shore (1%). A large portion (37% in north and 58% in south) of sphaeriidae were too small (< 1mm) to be identified and likely juveniles.

Mollusc biomass (not presented) followed similar trends to those described above for

Figure 6. Gastropod (a) (b), mussel (c) (d), and sphaeriidae clam (e) (f) densities on both shores (vertical dashed lines indicate agricultural tributary inputs).



densities. A notable exception was visible with the relative importance of the Viviparidae family. This family was negligible in term of density but, in account of the large individual size, represented 83% of gastropod biomass in the south shore. Viviparidae were absent from the north shore.

Total mollusc species richness ranged from 3 (site N5) to 23 (site S3) and tended to be higher at south shore sites than in the north shore (Table IV). Similar trends were observed when considering the *Shannon Diversity Index* and the *Pielou Evenness Index*. Both indices were lowest (0.04) at site N5 and reached their highest value (2.14 and 0.89, respectively) at site S2. Species richness and other measures of diversity were highest at sites where cumulative time of emersion was < 5 days (S0, S1, S2, S3, S5) and lowest at sites subjected to emersion lasting for 20 days or more (N1 to N6) (Table II). Within the latter group of sites, little difference in overall diversity was observed among sites exposed to emersion periods between 20 and 56 days.

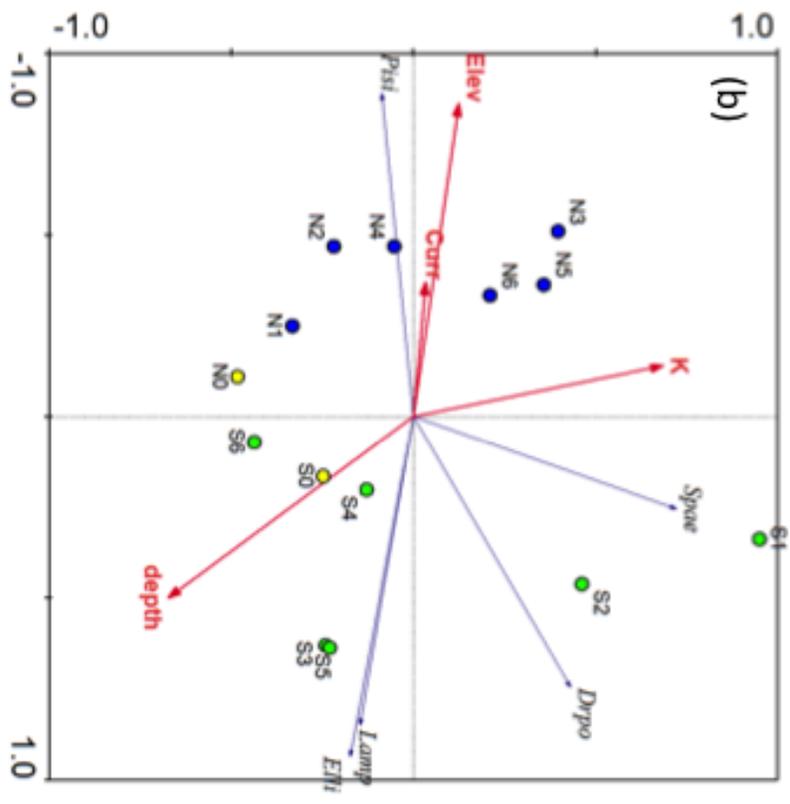
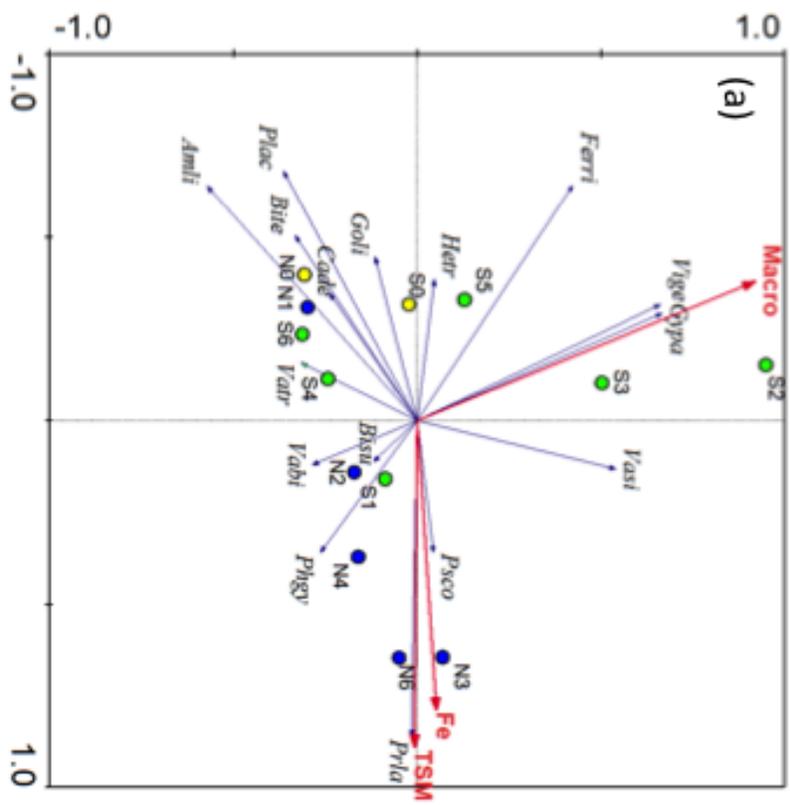
Models

Variables best explaining the taxonomic composition, density, biomass and diversity of the mollusc assemblages were identified using multivariate analyses (RDA) and stepwise multiple regressions. Gastropod species composition was best explained by total suspended matter ($p=0.003$) and dissolved iron ($p=0.041$), which were positively associated with *Probythinella lacustris* and negatively with *Amnicola limosa*, *Pleurocera acuta*, and *Ferrissia spp.* along the 1st axis (40% of total variance) of the RDA (Figure 7a). Axis II showed that 15% of the variance was explained by macrophyte biomass ($p=0.008$) closely associated with the

Table IV. Diversity indices (specific richness, *Shannon Diversity* & *Pielou Evenness*).

Sites	Specific Richness	<i>Shannon Diversity Index</i>	<i>Pielou Evenness Index</i>
N0	13	1.37	0.54
N1	10	0.42	0.18
N2	9	0.12	0.05
N3	7	0.39	0.22
N4	9	0.37	0.17
N5	3	0.04	0.04
N6	8	0.14	0.07
S0	12	1.71	0.69
S1	15	1.96	0.73
S2	11	2.14	0.89
S3	23	1.78	0.57
S4	14	1.63	0.62
S5	13	2.07	0.81
S6	12	1.32	0.53

Figure 7. Redundancy Analyses of composition of gastropod species (a) and bivalve genera (b). Arrows indicate the most influent variables, blue dots indicate north shore sites, green dots indicate south shore sites, and yellow dots indicate control sites.



occurrence of *Viviparus georgianus*, *Gyraulus parvus*, *Valvata sincera*, and *Ferrissia* spp. (Figure 7a).

For bivalve composition, (Figure 7b), the RDA indicated that 71% of the variance was explained by axis I represented by site elevation ($p=0.001$) and current velocity ($p=0.004$). The sphaerid clam *Pisidium* spp. was positively associated with this gradient whereas the unionid mussel *Elliptio* and *Lampsilis* were associated with low elevation and current velocity. Sampling depth ($p=0.043$) and the light extinction coefficient k ($p=0.023$) along axis II explained further 9% of the variance and were associated with the sphaerid clam *Sphaerium* spp.

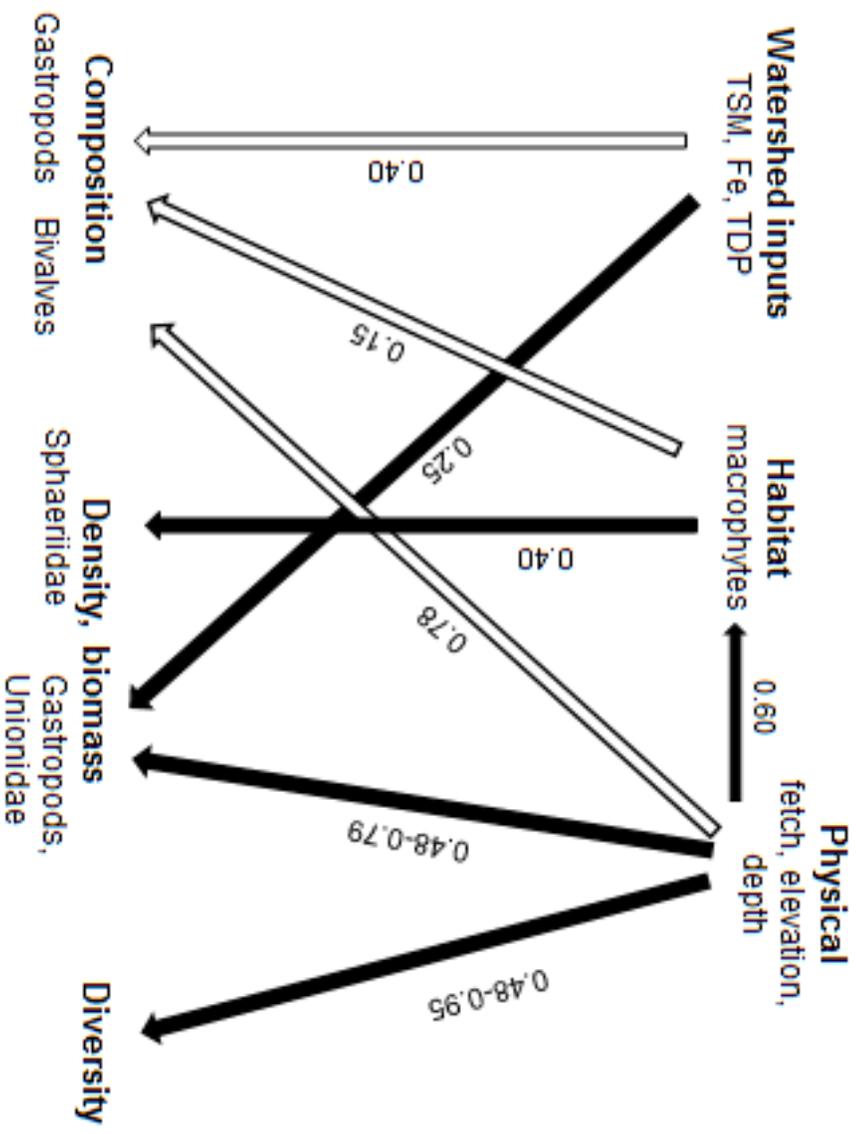
In stepwise multiple regressions, gastropod density was best predicted by SW fetch (-) and depth (+), unionidae density by elevation (-), NH_4 (-), and total dissolved phosphorus concentrations (+), and sphaeriidae density solely by macrophyte biomass (-). Similar results were obtained when multiple regression were calculated for biomass instead of density (Table V). South-West fetch was the variable best explaining (-) macrophyte biomass as well as specific richness, *Shannon Diversity*, and *Pielou Evenness* indices. Site elevation (-) also contributed to the explanation of these latter two indices (Table V).

A group of variables driving the spatial variations in mollusc composition, densities, biomass, and diversity were identified by the multivariate analyses and multiple regressions (Figure 8). Physical variables related to wind exposure (SW fetch) and site elevation stood out as the most important factors determining mollusks' species composition, diversity, abundance and biomass. Their effect may have been direct or indirect through the abundance of macrophytes that were strongly related (negatively) with fetch and site elevation. Water

Table V. Multiple regressions of gastropod, sphaeriidae, unionidae, macrophytes, and diversity indices (specific richness, *Shannon* and *Pielou Evenness*).

Dependent Variable	Equation	Adjusted R ²	P
Log Gastropod Density	-1.32 - 0.93 Log Fetch + 0.04 Depth	0.79	0.0001
Log Gastropod Biomass	-2.75 - 0.81 Log Fetch + 0.06 Depth + 0.11 Dtrib	0.79	0.0003
Log Sphaeriidae Density	1.94 - 0.27 Log Macro	0.40	0.0087
Log Sphaeriidae Biomass	0.77- 0.26 Log Macro	0.37	0.0118
Log Unionidae Density	15.73 - 5.12 Elev - 1.53 Log NH4 + 2 Log TDP	0.79	0.0003
Log Unionidae Biomass	41.84 - 12.53 Elev	0.48	0.0034
Log Macrophyte Biomass	1.29 - 2.30 Log Fetch	0.60	0.0007
Specific Richness	15.736 - 6.890 Log Fetch	0.48	0.0038
<i>Shannon Diversity Index</i>	9.415 - 2.672 Elev - 0.829 Log Fetch	0.95	< 0.00001
<i>Pielou Evenness Index</i>	4.030 - 1.072 Elev - 0.309 Log Fetch	0.87	< 0.00001

Figure 8. Main drivers of mollusc assemblages in Lake Saint-Pierre, Quebec, Canada. Positive relationships are represented by white arrows and negative relationships by filled arrows. The numbers indicate the variance explained (adjusted R^2) by the different set of drivers in RDA analyses (composition) and in multiple regressions (density, biomass, diversity).



quality variables describing watershed inputs linked to tributaries (TSM, Fe, k, TDP, NH₄) explained part of the taxonomic composition of gastropods, and a small but significant fraction of unionidae density, but were not significant in the other models of density, biomass, and diversity (Figure 8).

DISCUSSION

In this study, we hypothesized that molluscs in Lake Saint-Pierre would be affected by the inputs of agricultural tributaries and by physical drivers such as fetch and emersion regime. Our results indicated that physical environmental conditions indeed exerted the most important effect on density, biomass, and diversity of both gastropods and bivalves (Figure 8). This effect could have been direct or through habitat alteration, such as the reduction of submerged macrophytes induced by wind exposure and emersion events.

Effect of sediment drying out

Field observations and experimental evidences have linked severe decreases in native and non-native mollusc species with summer drought periods in the Rhine River (Collas et al. 2014). Bivalves were negatively affected by drawdowns in the Mississippi River and this effect was strongest for large individuals unable to fit into the interspaces between pebbles (Tucker et al. 1997). By virtue of their minute size, sphaerid clams can hide in interstitial spaces and have the ability to survive prolonged seasonal emersions in habitats where water levels vary unpredictably (Burky 1983; White 1979). Our results agree with these previous observations

showing a strong opposition between unionidae and spaeriidae along a gradient of elevation and exposure to periodical dessication.

Low water-level conditions (depth < 25 cm) during summer months may also result in exposure to extremely high water temperature (Hudon et al. 2010) that additionally reduces dissolved oxygen concentrations (Cremona et al. 2008). This hypoxia would particularly impact prosobranch snails and mussels which breathe dissolved oxygen. Low water levels can also affect mussel recruitment (Nalepa & Gauvin 1988) which could explain the lower abundance of mussels we observed at elevated sites.

Effect of fetch

In a study of several coastal wetlands subjected to different exposure to fetch, most molluscs were found in the protected sites (Burton et al. 2004). Higher taxonomic richness of invertebrate taxa was previously observed on the relatively protected south shore than on the exposed north shore of Lake Saint-Pierre (Tall et al. 2008). In our study, gastropod density and biomass were both negatively affected by fetch exposure. The most exposed sites were almost completely devoid of molluscs with the exception of sphaerid clams that reached their highest abundances. The above mentioned capacity of these clams to bury in the substrate to avoid scour together with their ability to survive in agriculturally degraded areas with high amounts of fine transported sediment (McMahon 1991) may explain their distribution.

Effect of submerged aquatic vegetation (habitat and food)

As previously observed in the St. Lawrence River (Hudon et al. 2010; Hudon et al. 2005), submerged macrophyte biomass was limited by a combination of elevation, water level

fluctuations, and fetch. The disappearance of submerged aquatic vegetation was previously observed in shallow sites of St. Lawrence River during the summer following dry episodes (Hudon 2004; Hudon 1997). The negative effects of fetch and elevation that we documented on the mollusc community could indeed be linked to the reduction in macrophytes that are crucial for many invertebrates. Gastropod density is positively related to macrophyte biomass (Strayer and Malcom 2007; Cyr and Downing 1988). Dense macrophyte beds could reduce fish predation (Marklund et al. 2002; Crowder and Cooper 1982) and lessen disturbance by waves and current (Green 2005; Madsen and Warncke 1983) while trapping detrital food (Rooke 1986). It is noteworthy that the highest mollusc abundance, species richness and occurrence of rare species were observed at site S3, which was nearly constantly underwater (1.4 day), was sheltered from dominant winds (2 km SW fetch) and supported a high macrophyte biomass. However, site S2 was characterized by similar chemical, physical variables, and a high plant biomass, yet supported a lesser mollusc abundance and biomass. This could be due to its location at the mouth of the Yamaska River, exposing this site to high turbidity (1237 ntu) and punctual disruption of organisms by high discharge events.

In our study, sphaeriidae clam density and biomass were negatively correlated with submerged macrophytes. This substantiates previous observations made in the Mississippi River that vegetation was generally associated with low sphaerid populations (Gale 1969). However, that study did also note that a few vegetated sampling sites supported remarkably high populations. Higher clam counts were found in regions with longer fetch and reduced vegetation than in sheltered backwater regions in the Upper Mississippi (Gray et al. 2005). This pattern was likely linked with differences in exchange rates at the sediment-water interface, which would increase with wind and be obstructed by vegetation. In a previous study of

sphaeriidae on the North shore of Lake Saint-Pierre, high densities were reported in the study area that was abundantly covered in *Vallisneria sp.* (Letarte 1985). The relationship between sphaeriidae and macrophytes deserves further study.

Effect of water quality degradation

Spikes in nutrient concentrations, total dissolved matter, and dissolved Fe were observed following the input of the tributaries on the two shores of Lake Saint-Pierre. Contrary to our initial hypothesis, these water quality alterations did not translate in changes in diversity, density, and biomass of molluscs. However, total suspended matter and dissolved iron were important drivers of gastropod species composition. Gastropods were also more diverse and abundant in an impacted marsh than in a reference marsh in Lake Huron (Kashian & Burton 2000). This pattern was likely linked with increased nutrients, which stimulates periphyton growth, the principal food source for snails.

Chemical variables (ammonium, iron, pH) measured at our sites were below the criteria for surface water quality (MDDEFP 2013). However, in half of our study sites (mainly the north shore) total phosphorus concentrations exceeded the provincial water quality criterion (30 µg P/L) to protect aquatic life in rivers, as was previously noted (Hudon & Carignan 2008). In our study, *Probythinella lacustris*, was the only gastropod species found to be positively associated with TSM and dissolved iron. According to Hilsenhoff's biotic index (1987), this snail is indeed tolerant of very significant organic pollution (Bode et al. 1996)

Our study underlines that the mollusc communities of Lake Saint-Pierre are facing multiple stressors. Increased interannual and seasonal variations in water level have been observed in the last few years (Hudon et al. 2010) and are predicted to intensify under climate

change scenarios. Large parts of the system will be exposed to emersion or to critically low water levels for macrophyte survival. Frequent wind episodes are also forecasted, which could scour the exposed sites along the north shore, especially when water levels are low. This dramatic situation is compounded with the presence of agricultural tributaries that increase total suspended matter and nutrients. Our study provides a benchmark for future studies that should monitor these communities, which are crucial for the maintenance of the fish, bird, and mammal populations of this large ecosystem.

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Chapitre 3: General Conclusion and Perspectives

Lake Saint-Pierre is a freshwater ecosystem of utmost interest and value. This fluvial lake of the St. Lawrence River is a nature reserve due to the extent of its wetlands and its important biodiversity. This lake is, however, subject to various environmental and anthropogenic pressures such as shoreline erosion, low water levels, agricultural tributary inputs, and the introduction of invasive aquatic species. Although Lake Saint-Pierre macroinvertebrate communities have been studied multiple times in the past (Tourville Poirier et al. 2010; Tall et al. 2008; Tessier et al. 2008), no recent study focused solely on the mollusc group as a whole in this fluvial lake.

This study examined the species composition, diversity, density, and biomass of the mollusc community in Lake Saint-Pierre as a benchmark for future evolution of this fluvial lake ecosystem. Our findings provide an understanding of the influence of water quality characteristics of agricultural tributaries (total suspended matter, dissolved iron, total dissolved phosphorus) and physical environmental conditions (fetch and elevation) on Lake Saint-Pierre habitats and in particular on molluscs, which constitute an important food resource for fish and birds.

Our study highlighted differences between environmental characteristics of the north and south shores of Lake Saint-Pierre, showing the impact of water level fluctuations, summer emersion periods and fetch on the mollusc assemblages along the north shore. With an

increase in extreme and unpredictable water level variations due to climate change, certain areas such as the north shore will continue losing its diversity and abundance not only in molluscs, but also in macroinvertebrates and submerged aquatic vegetation in general. This inevitably will have repercussions for animal taxa higher up the trophic food chain such as fish and birds that feed mainly on macroinvertebrates. Loss of aquatic vegetation habitat and lower food resources on the north shore could partially account for the observed decline of fish species such as the Yellow Perch in Lake Saint-Pierre. Recurrent low water levels over several years could have severe consequences not only for fish populations, but also for local fisheries that depend on them. These extreme events might enhance the distribution of tolerant or non-native mollusc (i.e. *Dreissena polymorpha*) and plant species. The south shore, however, appeared more vulnerable to zebra mussel invasion.

We also emphasized the low abundance of submerged macrophytes observed on the north shore, which contrasts with the abundance of aquatic vegetation on the south shore. It might be interesting to verify the biomass of macrophytes observed on the north shore with historical data. A low biomass of macrophytes possibly could have been observed on the south shore if we had selected and sampled an area characterized by periodic emersion events. It is also possible that the north-eastern area of Lake Saint-Pierre has very few macrophytes regardless of water level fluctuations due to the presence of fast water currents and clay.

Our sampling took place over a period of two weeks in the late summer. This particular season was chosen because it corresponds to the end of the growth period for most juvenile gastropods from the spring generation, and it also takes into account individuals born during the summer. This short observation period, however, could limit the range of observable

environmental influences on mollusc populations. For future studies, it would be recommended to spread out several samplings over a year in order to obtain additional information on possible environmental conditions that could seasonally influence molluscs in Lake Saint-Pierre.

During the sampling along the north shore, the water level was high and the following week, the water level had dropped which allowed us to sample at lower elevations along the south shore. We could have improved sampling by randomly choosing sites and by sampling sites from both shores in a same day. This was done in part with site N0 that was sampled on the same day as site S5 on the south shore. In our results, it is difficult to distinguish the relative effects of elevation from those pertaining to fetch. We should have compared sites with similar emersion events, but with different exposures to fetch. It is also difficult to attribute the different mollusk abundances between both shores to physical-chemical differences without being able to eliminate the effect of emersion which was observed uniquely on the north shore. Otherwise, multiple regression analyses could have been done to distinguish the relative importance of elevation, fetch and macrophytes on mollusc abundance.

Very few juvenile unionid mussels were found in our study, as shown by the detailed size composition of bivalves (Appendix XIX). These juveniles are known to burrow deeper into the sediment than do adults. Sampling with a dipnet may have limited our ability to sample deep enough to thoroughly collect these juveniles, following the sampling methods used for our study (Appendix II). Other factors affecting unionid mussel recruitment could be related to the extremely low water levels recently observed on the north shore, and the availability of fish hosts for the glochidial larval stage. The majority of the unionid mussel species sampled in our study depend mainly on fish such as perch and sunfish to complete

their lifecycle. The observed decline in Yellow Perch, *Perca flavescens*, in Lake Saint-Pierre most likely had subsequent consequences on unionid mussel populations. Additional studies should be carried out to investigate possible relations between Yellow Perch and unionid mussel densities. It would also be worth investigating the abundance and diversity of mussel host fishes on the north shore to see if it could partly explain the very low abundance and species richness of mussels in that area. A comparison of unionid mussel species composition should also be done between the fluvial lakes of the St. Lawrence to determine how the situation we reported in Lake Saint-Pierre compares with other areas of the St. Lawrence River.

It has been previously shown that gastropods were negatively associated with the occurrence of nitrogen-fixing filamentous cyanobacteria, *Lyngbya wollei* (Tourville-Poirier et al. 2010). However, at south shore sampling site S1, uniquely characterized by a high biomass (41 g dry mass/m²) of *Lyngbya* (see details in Appendix IV) we observed the second highest abundance (56 individuals/m²) of gastropods in our study. However, this site was surnamed "the mollusc cemetery" due to the presence of multitudes of remnant shells of gastropods and mussels, with a portion that had died recently (nacre is always lustrous in fresh shells). For the most part, dead mollusc individuals were far more abundant than live ones. Most individuals belonging to the unionid mussel genera *Elliptio* (81%) and *Lampsilis* (89%) sampled at site S1 were dead, although the invasive zebra mussel, *Dreissena polymorpha*, appeared more resistant to this particular habitat with only 47% dead individuals. It is also worth noting that this specific site had the highest zebra mussel abundance (7 individuals/m²) in our study. Although our analyses concerned only live individuals, the size structure of dead organisms could be investigated. The causes underlying this high mollusc mortality and what may still be

causing this on-going situation at this specific area could be a subject of interest for future studies. These zebra mussels could be contributing to the proliferation of this filamentous cyanobacterium in this area, as previously observed in an experiment by Armenio (2011). Characterized by a low abundance (2 g dry mass/m²) of macrophytes, the surprisingly high abundance of live gastropods inhabiting this site could be due to the extent of alternative substrates suitable for periphyton colonization: the dead mollusc shells.

In our study, the abundance of the invasive snail, *Bithynia tentaculata*, only ranged from 0.2 to 5 individuals/m². Such low density is in sharp contrast with the abundance reported in earlier studies (Pinel-Alloul et al. 1996; Lamarche et al. 1982; Magnin 1970), indicating that this taxon was the most abundant gastropod in the St. Lawrence River. This finding could indicate a decline in this invasive gastropod species, which should be confirmed by supplemental studies in other fluvial lakes of the St. Lawrence River such as lakes Saint-Louis and Saint-François. It would also be interesting to verify the consistency of mollusc identifications throughout samples from previous studies in Lake Saint-Pierre.

Previous studies mostly took place along the south shore of Lake Saint-Pierre (Tourville Poirier et al. 2010). More studies should be done to further characterize the north shore and the various environmental pressures endured by macroinvertebrate and aquatic vegetation communities. It is likely that other macroinvertebrate populations in this fluvial lake will have similar responses to water level fluctuations, desiccation periods, and wave exposure as molluscs. It would be interesting to pursue studies on the mollusc assemblages for both shores at regular time intervals in order to observe long-term trends or changes in relation to environmental variables. In order to further study the relation between elevation and

molluscs, future studies could survey areas along several transects from the shallow inshore areas going towards deeper sites away from the shore.

Overall, molluscs are becoming more vulnerable due to anthropogenic impacts and environmental perturbations that occur in freshwater habitats. This is a cause for concern because this group of macroinvertebrates play an essential and non-negligible role in the functioning of these ecosystems.

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Appendix I. Mollusk species found in St.Lawrence River (1) Peckarsky et al. 1990, (2) Pinel-Alloul & Magnin 1973, (3) Pinel-Alloul & Magnin 1979, (4) Pinel-Alloul et al. 1996, (5) Farrell et al. 2010, (6) Lacoursière et al. 1975, (7) Vincent 1979 (8) Projet Archipel, (9) Nalepa & Gauvin 1988, (10) Magnin 1970, (11) Alain Armellin, (12) Desrosiers et al. 2008.

Taxon	Family	Species	Observation Site	Reference
Prosobranchia (Caenogastropoda)	Bithyniidae	<i>Bithynia tentaculata</i>	Lake St-François Lake St-Louis Lake St-Pierre	(4) (8) (10) (11)
		<i>Ammicola limosa</i>	Lake St-Louis Lake St-François Lake St-Pierre	(2) (4) (1) (8) (10) (11)
Hydrobiidae		<i>Ammicola walkeri</i>	Lake St-Pierre	(11)
		<i>Birgella subglobosa</i>	St-Lawrence River	(1) (12)
		<i>Gillia altilis</i>		(1)
		<i>Probythinella emarginata</i>	Lake St-Pierre	(11)
		<i>Probythinella lacustris</i>	Lake St-François	(4) (8)
		<i>Goniobasis livescens</i>	Lake St-François Lake St-Louis Lake St-Pierre	(4) (1) (8) (10) (11)
		<i>Pleurocera acuta</i>	Lake St-François Lake St-Pierre	(4) (11)
Valvatiidae		<i>Valvata lewisi</i>	St-Lawrence River	(12)
		<i>Valvata piscinalis</i>	Lake St-François Lake St-Pierre	(4) (1) (11)
		<i>Valvata sincera</i>	Lake St-François	(4) (1) (8)
		<i>Valvata tricarinata</i>	Lake St-François Lake St-Louis	(4) (1) (8) (10)

Pulmonata	Viviparidae	<i>Cameloma decisum</i>	St-Lawrence River	(6) (1) (8)		
		<i>Cipangopaludina chinensis</i>	St-Lawrence River	(1) (12)		
		<i>Viviparus georgianus</i>	St-Lawrence River	(7) (1)		
		<i>Viviparus intertextus</i>		(8)		
		<i>Ferrisia parallela</i>	Lake St-Louis Lake St-Pierre	(8) (10) (11)		
Lymnaeidae	Ancyliidae	<i>Ferrisia rivularis</i>		(1) (8)		
		<i>Acella haldemani</i>		(1)		
		<i>Bulinnea megasoma</i>		(1)		
		<i>Fossaria</i>	Lake St-Pierre	(1) (11)		
		<i>Lymnae stagnalis</i>		(1) (8)		
		<i>Pseudosuccinea columella</i>	Lake St-Pierre	(1) (8) (11)		
		<i>Stagnicola catascopium</i>	Lake St-Louis	(1) (3) (8) (10)		
		<i>Stagnicola elodes</i>	Lake St-François	(4) (7) (8) (12)		
		Physidae	Physidae	<i>Aplexa elongata</i>		(1)
				<i>Physa gyrina</i>	Lake St-François Lake St-Louis	(4) (1) (8) (10)
<i>Physa heterostropha</i>				(1)		
<i>Physa integra</i>	St-Lawrence River			(1) (12)		
<i>Armiger crista</i>	Lake St-Pierre			(4) (8) (11)		
Planorbidae	Planorbidae	<i>Gyraulus deflectus</i>	Lake St-François	(4) (1) (8)		
		<i>Gyraulus hirsutus</i>	Lake St-Louis	(8) (10)		
		<i>Gyraulus parvus</i>	Lake St-François	(4) (1) (8) (10)		
			Lake St-Louis			
		<i>Helisoma anceps</i>	Lake St-François	(4) (1) (8) (10)		

Unionidae	<i>Alasmidonta heterodon</i>		(1)
	<i>Alasmidonta marginata</i>		(1)
	<i>Amblema plicata</i>	Lake St-Clair	(9)
	<i>Anodonta cataracta</i>		(1)
	<i>Anodonta grandis</i>	Lake St-Clair	(9) (1) (8)
	<i>Anodontoides ferussacianus</i>		(1)
	<i>Elliptio complanata</i>	Lake St-Louis	(4) (1) (8) (10)
	<i>Elliptio dilatata</i>	Lake St-Louis Lake St-Clair	(1) (10) (9)
	<i>Fusconata flava</i>	Lake St-Clair	(9)
	<i>Lampsilis cariosa</i>		(1)
	<i>Lampsilis fasciola</i>	Lake St-Clair	(9)
	<i>Lampsilis ovata</i>		(1) (8)
	<i>Lampsilis radiata</i>	Lake St-Louis Lake St-Clair	(10) (1) (8) (9)
	<i>Lampsilis siliquoides</i>		(1)
	<i>Lampsilis ventricosa</i>	Lake St-Clair	(9)
	<i>Lasnigona complanata</i>	Lake St-Clair	(9)
<i>Lasnigona compressa</i>		(1)	
<i>Lasnigona costata</i>		(1)	
<i>Leptodea fragilis</i>	Lake St-Clair	(1) (9)	
<i>Ligumia nasuta</i>	Lake St-Clair	(1) (9)	
<i>Ligumia recta</i>	Lake St-Clair	(1) (9)	
<i>Obovaria olivaria</i>		(1)	
<i>Obovaria subrotunda</i>	Lake St-Clair	(9)	

	<i>Pleurobema cordatum</i>	Lake St-Clair	(9)
	<i>Proptera alata</i>	Lake St-Clair	(1) (9)
	<i>Quadrula quadrula</i>	Lake St-Clair	(9)
	<i>Strophitus undulatus</i>	Lake St-Clair	(1) (9)
	<i>Truncilla donaciformis</i>	Lake St-Clair	(9)
	<i>Truncilla truncata</i>	Lake St-Clair	(9)

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Appendix II. Detailed methods.

Laboratory sorting and identification of samples

First, we sorted through each sample, grouped and counted the molluscs by families in individual vials per replicate. Samples with macrophytes were first examined with the naked eye, and then the sediment part was examined under the dissecting microscope at the 6X magnification.

A representative subset of the other non-mollusc macroinvertebrates were grouped together in one vial per replicate, while taking into account the relative abundance of the different groups (Gammaridae, Chironomidae, oligochaetes, etc ...) using log-scale classes: (-) absence of individuals, (+) <10 individuals, (++) 10-100 individuals, and (+++) >100 individuals.

Eventually, we went back through each family of molluscs and identified all individuals to the furthest taxonomic level possible. The Bithyniidae, Hydrobiidae, Lymnaeidae, Planorbidae, Pleuroceridae, Valvatidae, Viviparidae, Dreisseniidae, and Unionidae families were identified to the species level, whereas the Ancyliidae and the Sphaeriidae were only identified to the genus level. Juvenile individuals from the Sphaeriidae family were not sufficiently well developed for identification to the genus level. In order to separate larger individuals from these smaller juveniles, we sieved each replicate sample through a 1mm mesh. The *Freshwater macroinvertebrates of Northeastern North America* (Peckarsky et al. 1990) and *The Freshwater Molluscs of Canada* (Clarke 1981) were the guides used for mollusc identification. The density of each mollusc family was averaged per

site (mean \pm s.d.) and converted per unit of sampling effort. Mollusc samples were converted per m² of sampled surface area: 4 m x 0.3 m (net width).

Laboratory Mollusc Measurements

-Unionidae and Dreissenidae marking and measurements:

For all individuals of each replicate, we measured the length, height, and the thickness of the shell with a digital vernier (± 0.5 mm precision). The length was measured along the longest anterior-posterior axis between the umbo and the exterior extremity of the valves. The height was measured along the maximal distance between the dorsal and the ventral sides of the shell. The thickness (width) of the bivalve was measured along the maximal distance between both exterior sides of both valves.

Each individual was marked with an identification number on an index card that was inserted inside the shell and on another card attached to the exterior of the shell with a rubber band. These bivalves were also identified to the species level. The data for each individual (replicate number, sampling site, sampling date, identification number, length, height, thickness, species) were logged into an excel spreadsheet. For unionid mussels smaller than 7 mm in length, their dimensions were measured with *Image-Pro Plus 7.0* digital microscope imagery.

Empty shells of unionid and dreissenid mussels were identified, counted, and measured with the same methods used for live mussels. The presence of a full shell or an individual valve was noted. For the thickness measurement for individual valves, an index card was put

along the inside and the measure will be doubled after. Each shell or valve was marked with an identification number inside with a permanent marker.

-Sphaeriidae measurements:

The length was measured for Sphaeriidae clams using *Image-Pro Plus 7.0* digital microscope imagery. All intact (unbroken) individuals in each sample replicate were measured. However, only a subset of the replicates was measured when samples had more than 300 individuals in certain replicates. This subset was deemed representative of the non-measured ones.

-Gastropod measurements:

For all intact (unbroken) individuals of each replicate, we measured a specific body dimension (mm): shell height, shell width, or aperture width. Shell height was measured for all gastropods except the Planorbidae and Ancyliidae families. Shell width was measured for the planorbids and aperture width was measured for the ancyliids. The larger gastropods such as the Viviparidae family were measured with a digital vernier whereas the other smaller ones, were measured with *Image-Pro Plus 7.0* digital microscope imagery.

Mollusc Biomass

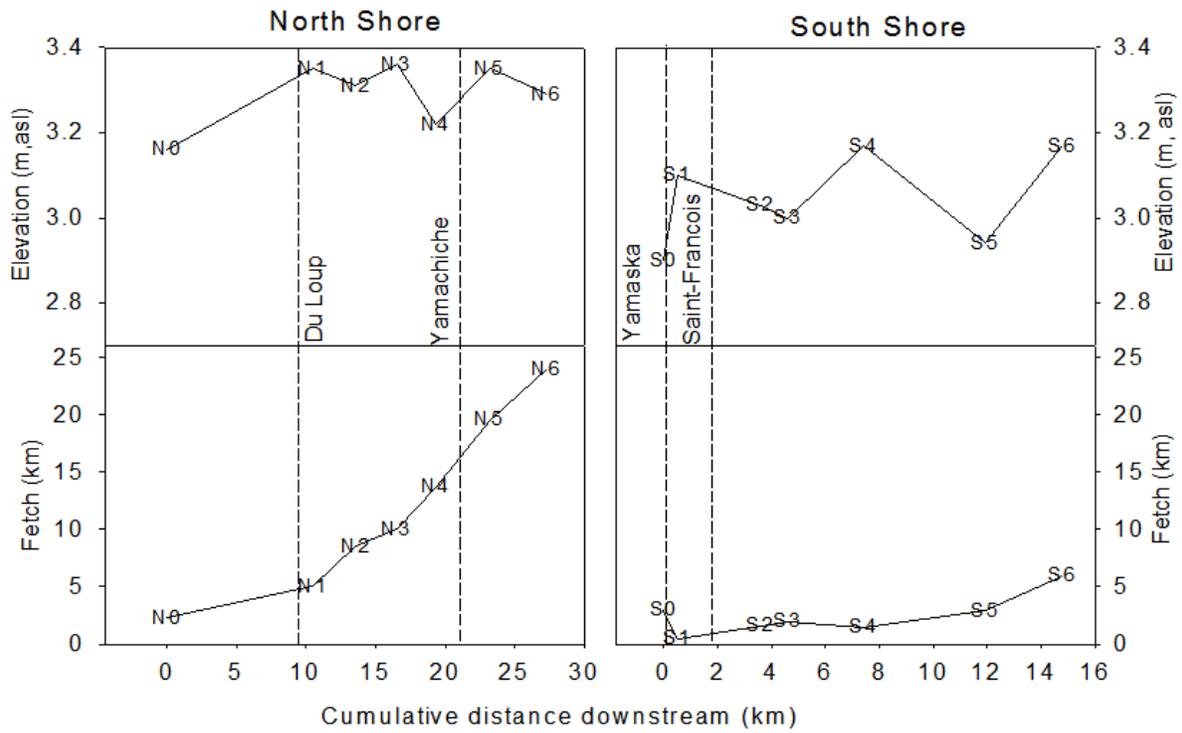
Measurement of individuals from each taxon collected at each site was carried out to assess and compare biomass among sites. Body dimensions (mm) were converted to biomass using previously published conversion equations for each taxon (Méthot et al. 2012; Ozersky et al. 2012; Benke et al. 1999; Balfour & Smock 1995; Mackie 1991; Cameron et al. 1979; Greig, unpublished data). For each replicate, we corrected the total biomass measured to

account for the individuals that were not measured (broken or lost). First, we calculated the percentage of measured individuals over counted individuals, and then the biomass was corrected as such: $(\text{biomass measured} * 100) / (\% \text{measured} / \text{counted})$. For the equations from Méthot et al. 2012 (Ancylidae, Bithyniidae, Physidae, Planorbidae, Valvatidae, and Viviparidae families), we multiplied the biomass by 0.2 to obtain the tissue biomass without the shell (20% tissue, 80% shell).

Appendix III. Conversion equations to determine mollusc biomass (mg DM).

Taxa	Equation	Reference
Ancylidae	$\text{LOG}_{10} \text{ DM} = -1.54 + 2.7 * (\text{LOG}_{10} (\text{aperture width mm}))$	Méthot et al. 2012
Bithyniidae	$\text{LOG}_{10} \text{ DM} = -0.57 + 2.5 * (\text{LOG}_{10} (\text{Shell height mm}))$	Méthot et al. 2012
Hydrobiidae	$\text{LOG}_{10} \text{ DM} = -0.74 + 2.82 * (\text{LOG}_{10} (\text{Shell height mm}))$	Méthot et al. 2012
Lymnaeidae	$\text{DM} = (0.046 * ((\text{Shell height mm})^3 * 2341)) * 0.85$	Greig, unpublished data
Physidae	$\text{LOG}_{10} \text{ DM} = -1.34 + 3.05 * (\text{LOG}_{10} (\text{Shell height mm}))$	Méthot et al. 2012
Planorbidae	$\text{LOG}_{10} \text{ DM} = -1.12 + 2.9 * (\text{LOG}_{10} (\text{Shell width mm}))$	Méthot et al. 2012
Pleuroceridae	$\text{DM} = 0.0134 * ((\text{Shell height mm})^2 * 5841)$	Ozersky et al. 2012
Valvatidae	$\text{LOG}_{10} \text{ DM} = -0.93 + 3.18 * (\text{LOG}_{10} (\text{Shell height mm}))$	Méthot et al. 2012
Viviparidae	$\text{LOG}_{10} \text{ DM} = -0.64 + 2.6 * (\text{LOG}_{10} (\text{Shell height mm}))$	Méthot et al. 2012
Dreissenidae	$\text{DM} = 0.007 * ((\text{Shell length mm})^2 * 982)$	Mackie 1991
Elliptio	$\text{DM} = 0.0023 * ((\text{Shell length mm})^3 * 156)$	Balfour & Smock 1995
Lampsilis	$\text{DM} = -0.0075 * ((\text{Shell length mm})^2 * 931)$	Cameron et al. 1979
Sphaeriidae	$\text{DM} = 0.0163 * ((\text{Shell length mm})^2 * 477)$	Benke et al. 1999

Appendix IV. Physical (elevation, fetch) at sampling sites located at increasing distance downstream along the north and south shores of Lake Saint-Pierre (Dotted lines indicate agricultural tributary inputs).

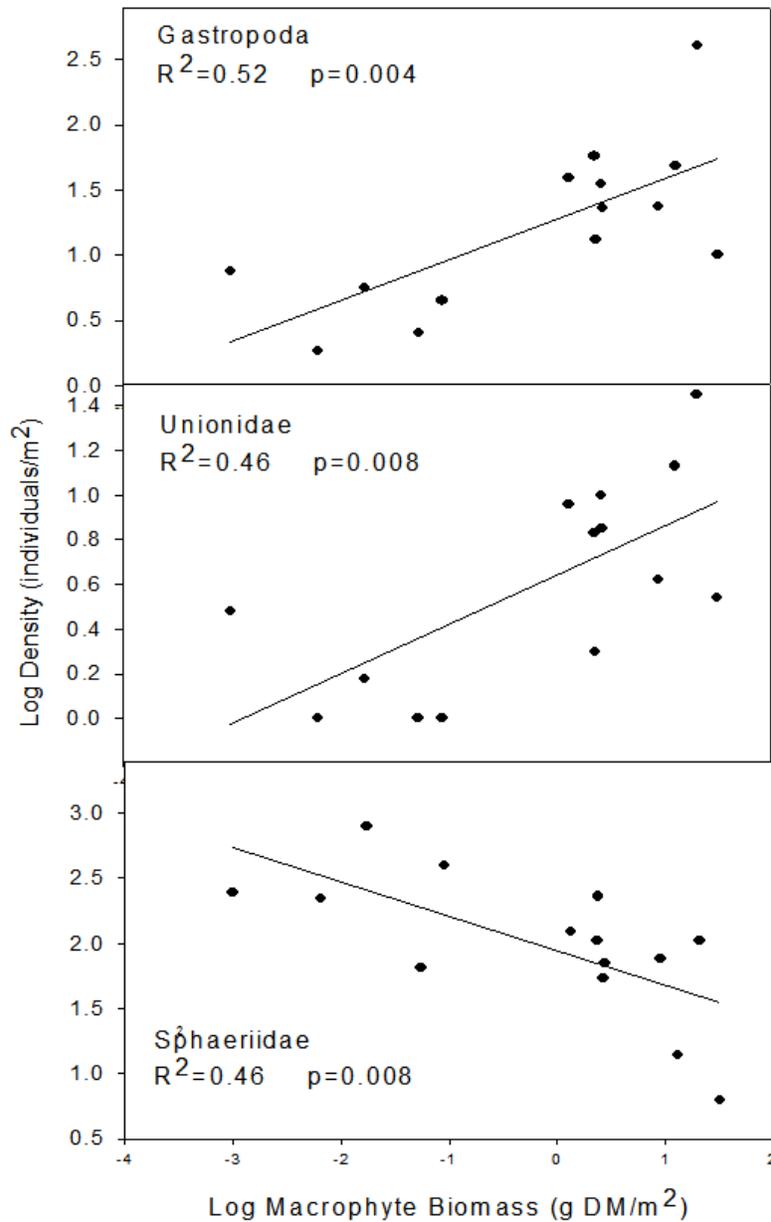


Appendix V. Morphometry, sediment characteristics, aquatic vegetation, and water physical/chemical variables of each sampling site.

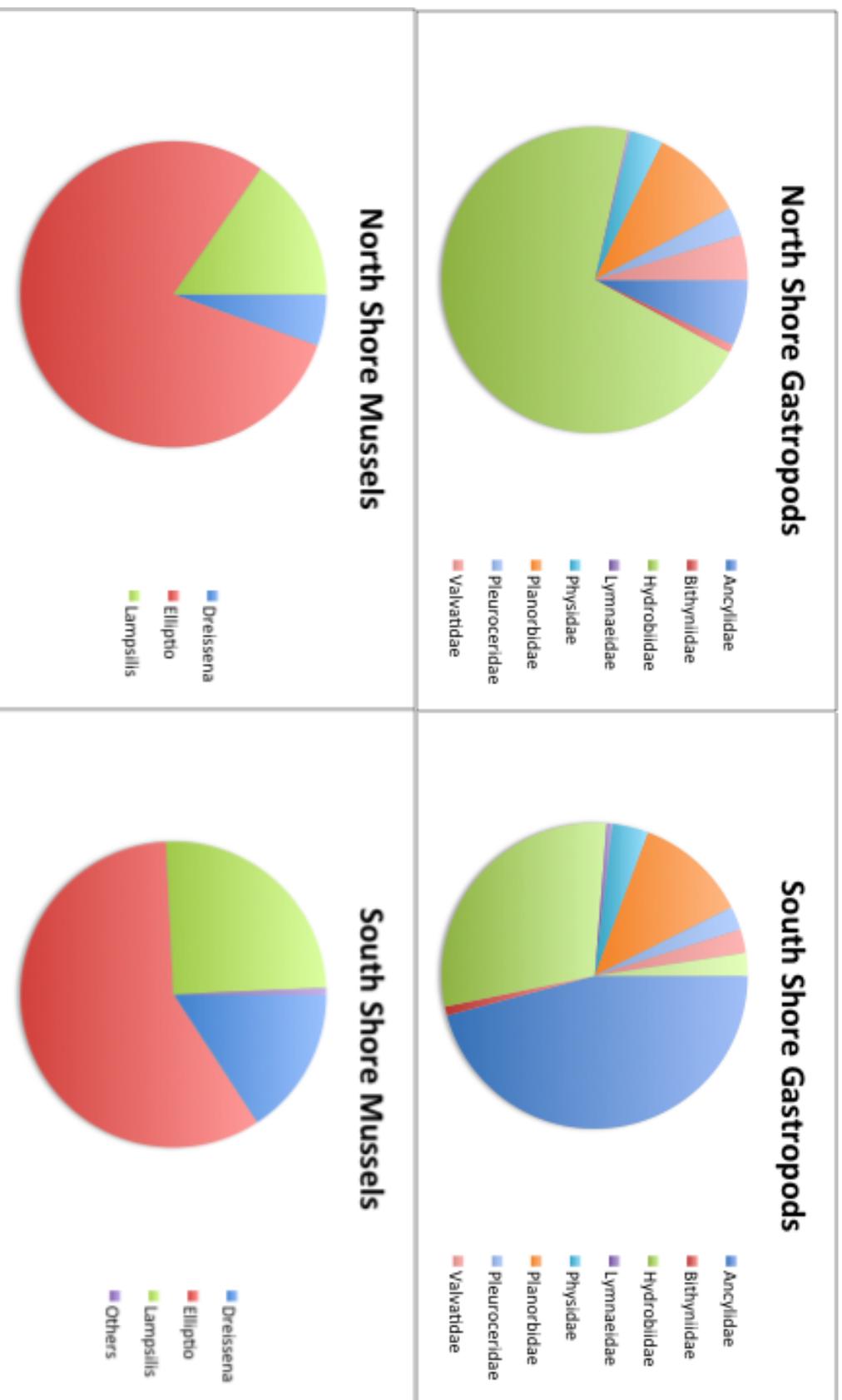
		North Shore										South Shore					
		NO	N1	N2	N3	N4	N5	N6	S0	S1	S2	S3	S4	S5	S6		
Sampling Site																	
Depth (cm)		77	70	75	70	75	68	71	80	60	70	100	84	87	83		
Temperature (Celsius)		16.50	20.47	20.07	19.04	17.12	16.79	17.89	19.53	19.79	18.72	14.57	14.53	14.44	15.03		
Conductivity (µS/cm)		220	174	180	154	136	189	174	218	269	170	144	186	175	166		
pH		7.53	7.97	7.58	7.20	6.82	7.12	7.69	8.08	7.96	7.32	8.00	7.94	7.88	8.32		
Turbidity (ntu)		1638.0	1247.2	849.3	527.6	520.1	1297.7	1075.0	1321.7	987.2	1236.8	31.8	1270.0	1282.2	1000.8		
Secchi Depth (cm)		fond	>70	70	40	38	36	35	>80	40	>70	80	fond	fond	fond		
Current Velocity (m/s)		9.2	2.2	9.8	9.8	15.4	6.9	9.2	18.6	7.0	6.7	2.6	2.9	5.6	4.9		
K: light extinction coefficient (m-1)		0.737	0.846	2.666	5.020	3.348	4.159	3.796	1.448	3.886	2.839	4.191	3.097	1.871	1.659		
Sediment Characteristics	Gravel (%)	0.00	0.00	0.0	0.12	0.0	N/A	0.02	0.00	2.84	0.00	0.00	0.23	0.00	1.09		
	Sand (%)	96.63	97.49	85.2	90.03	83.2	N/A	89.93	89.20	93.06	85.77	78.71	96.53	96.13	96.79		
	Silt (%)	2.14	0.72	9.2	7.34	13.4	N/A	8.27	7.32	5.01	6.93	15.03	2.55	3.03	1.43		
	Clay (%)	1.23	1.80	5.5	2.62	3.4	N/A	1.80	3.48	1.93	7.30	6.26	0.91	0.84	1.78		
	DO %	101.4	105.9	95.8	97.3	90.5	111.2	102.7	99.9	102.0	99.1	106.0	109.4	105.1	107.1		
Chemical Variables	Water Color (Pt/Co)	17	28	38	42	72	129	145	23	41	68	80	57	40	55		
	Total Suspended Matter (mg N/L)	<1	2	36	73	24	68	38	5	33	9	6	1	2	5		

	Ammonium (mg N/L)	<0.003	0.006	0.029	0.021	0.016	0.077	0.053	0.044	0.026	0.023	0.042	0.006	0.006	0.004
	TN (mg N/L)	0.29	0.85	0.58	0.61	0.54	1.79	0.95	0.55	1.10	0.85	0.95	0.55	0.48	0.62
	TDN (mg N/L)	0.26	0.32	0.51	0.39	0.42	1.72	0.79	0.49	1.00	0.85	0.89	0.47	0.42	0.56
	Nitrites-Nitrates (mg N/L)	<0.02	<0.02	0.17	0.12	0.14	1.21	0.39	0.22	0.61	0.38	0.32	0.09	<0.02	0.11
	TP (ug P/L)	8	18	58	153	60	174	85	24	83	30	40	23	15	23
	TDP (ug P/L)	6	14	25	21	32	52	55	12	34	21	25	13	11	14
	Dissolved Ca (mg Ca/L)	22.5	17.6	18.6	13.4	9.7	11.9	12.5	23.1	28.9	19.3	17.8	21.2	19.3	19.5
	DOC (mg C/L)	4.0	5.5	5.0	4.7	4.3	7.2	5.1	4.0	5.5	10.7	10.9	8.7	8.5	9.6
	Diss. Fe (mg Fe/L)	0.074	0.150	0.217	0.306	0.576	0.926	0.693	0.115	0.270	0.253	0.325	0.353	0.139	0.188
	Phytoplankton Chlorophyll-a (ug/L)	0.77	1.08	2.17	7.97	3.26	4.23	3.41	2.48	5.33	1.69	1.43	1.22	2.03	3.15
	Submerged Macrophyte Biomass (g/m ²)	2.76	2.38	0.09	0.05	0.00	0.01	0.02	9.09	2.35	32.07	20.86	2.71	13.18	1.35
	Submerged Green Algae Biomass (g/m ²)	0.00	0.00	0.11	0.00	0.00	0.00	0.00	0.06	0.00	0.01	0.28	0.01	0.00	0.00
	Submerged Lyngbya Biomass (g/m ²)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.09	40.74	0.00	0.39	0.00	0.17	0.00

Appendix VI. Logarithmic relationships, between the total areal biomass (log g DM/m²) of gastropods (top panel), unionid mussels (middle panel), sphaeriidae clams (bottom panel), and macrophyte biomass (log g DM/m²). (For each relationship, the coefficient of determination (R²) and probability (p) are indicated).



Appendix VII. Gastropod family and mussel genera composition (densities) for both shores of Lake Saint-Pierre.



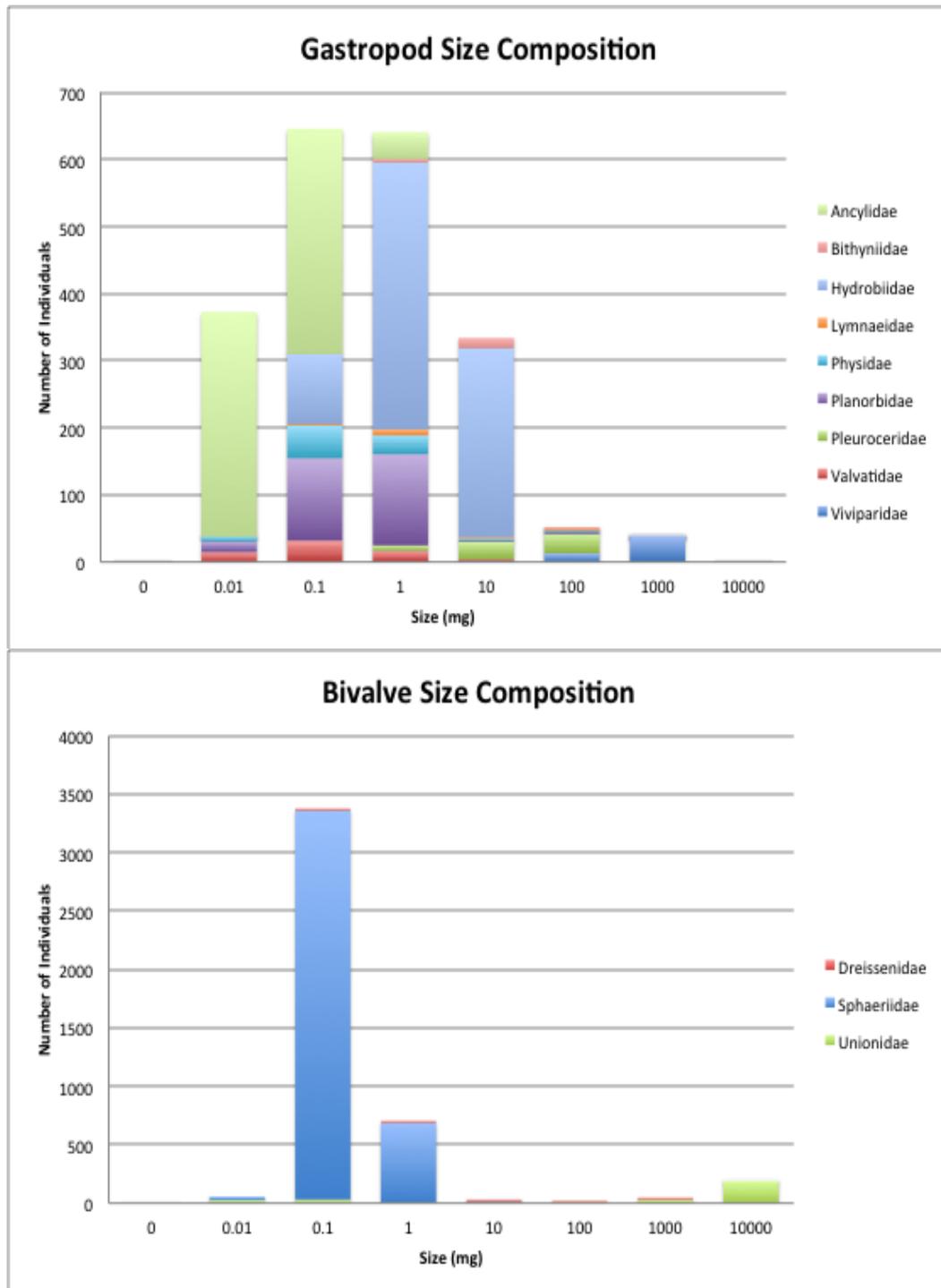
Appendix VIII. Total number of species per site in Lake Saint-Pierre.

Sites	Gastropods	Sphaeriidae	Unionidae	Dreissenidae
N0	9	1	2	1
N1	8	1	1	0
N2	7	2	0	0
N3	5	2	0	0
N4	5	2	2	0
N5	1	2	0	0
N6	5	2	1	0
S0	9	2	1	0
S1	10	2	2	1
S2	6	2	2	1
S3	16	2	4	1
S4	10	2	2	0
S5	9	1	2	1
S6	9	1	2	0

Appendix XIX. Size (mg) range of mollusc families in Lake Saint-Pierre with mean, standard deviation, and total number of individuals (N).

Family	Min size (mg)	Max size (mg)	Mean size (mg)	Standard Deviation	N
Ancylidae	0.0008	0.2	0.02	0.03	711
Bithyniidae	0.3	15.0	4.0	4.4	23
Hydrobiidae	0.02	3.8	0.8	0.7	784
Lymnaeidae	0.07	47.7	5.1	13.2	15
Physidae	0.003	17.9	0.6	2.3	89
Planorbidae	0.0009	18.1	0.3	1.4	279
Pleuroceridae	0.3	49.4	12.8	13.6	64
Valvatidae	0.001	4.1	0.2	0.6	66
Viviparidae	8.6	317.4	154.9	71.7	54
Dreissenidae	0.02	169.1	36.3	47.8	49
Sphaeriidae	0.006	5.5	0.07	0.2	4053
Unionidae	0.001	7133.8	1562.9	1275.3	296

Appendix XX. Gastropod and Bivalve Size Composition in Lake Saint-Pierre.



Appendix XI. Gastropod densities (individuals/m²) for each sampling site.

Site	ANCY	BITH	HYDR	LYMN	PHYS	PLAN	PLEU	VALV	VIVI	GAST
N0	1.1	0.3	16.7	0.0	0.3	1.1	1.4	1.1	0.0	21.9
N1	1.2	0.2	6.3	0.0	0.7	3.7	0.2	0.2	0.0	12.3
N2	0.2	0.0	2.5	0.0	0.3	0.0	0.0	0.5	0.0	3.5
N3	0.0	0.0	1.0	0.2	0.2	0.2	0.0	0.0	0.0	1.5
N4	0.3	0.0	6.0	0.0	0.0	0.0	0.0	0.3	0.0	6.7
N5	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.8
N6	0.0	0.0	3.8	0.0	0.3	0.2	0.0	0.3	0.0	4.7
S0	9.5	0.0	6.0	0.3	0.7	2.5	2.2	1.3	0.0	22.5
S1	8.1	0.0	37.2	0.3	2.8	3.6	0.6	3.3	0.6	56.4
S2	1.5	0.0	1.8	0.0	0.0	4.0	0.0	1.3	0.3	9.0
S3	240.0	4.7	66.4	2.8	16.1	56.7	4.4	7.2	10.0	408.3
S4	2.2	0.0	26.7	0.0	1.7	0.8	0.6	1.9	0.8	34.7
S5	18.1	0.0	15.0	0.0	1.9	5.6	3.3	0.3	2.8	46.9
S6	2.8	1.1	28.3	0.6	0.3	0.3	4.2	0.0	0.3	37.8

Appendix XII. Bivalve densities (individuals/m²) for each sampling site.

Site	DREI	SPHA	PISI	SPUM	SSPP	UNIO	ELLI	LAMP	LEPT	STRO	MOLL
N0	0.6	69.4	38.6	0.0	30.6	6.1	5.6	0.6	0.0	0.0	98.1
N1	0.0	228.3	141.0	0.0	87.2	1.0	1.0	0.0	0.0	0.0	241.7
N2	0.0	401.5	290.3	1.7	109.5	0.0	0.0	0.0	0.0	0.0	405.0
N3	0.0	63.7	29.2	1.3	33.2	0.0	0.0	0.0	0.0	0.0	65.2
N4	0.0	243.7	118.0	0.8	124.8	2.0	1.5	0.5	0.0	0.0	252.3
N5	0.0	218.0	149.3	0.2	68.3	0.0	0.0	0.0	0.0	0.0	218.8
N6	0.0	784.5	484.8	6.5	293.2	0.5	0.0	0.5	0.0	0.0	789.7
S0	0.0	74.3	22.7	0.2	51.5	3.2	3.2	0.0	0.0	0.0	100.0
S1	7.2	102.8	39.4	6.1	57.2	5.8	5.3	0.6	0.0	0.0	172.2
S2	1.2	5.3	2.5	0.2	2.7	2.5	1.8	0.7	0.0	0.0	18.0
S3	2.5	103.1	34.4	3.3	64.7	27.5	16.9	10.0	0.3	0.3	541.4
S4	0.0	52.5	25.3	0.8	26.4	8.9	6.1	2.8	0.0	0.0	96.1
S5	1.9	12.8	5.6	0.0	7.2	12.5	8.6	3.9	0.0	0.0	74.2
S6	0.0	121.9	55.3	0.0	66.7	8.1	5.6	2.5	0.0	0.0	167.8

Appendix XIII. Gastropod biomasses (mg DM/m²) for each sampling site.

Site	ANCY	BITH	HYDR	LYMN	PHYS	PLAN	PLEU	VALV	VIVI	GAST
N0	0.0	3.6	14.5	0.0	0.0	0.2	7.2	0.6	0.0	26.1
N1	0.0	2.5	2.6	0.0	0.0	0.5	0.1	0.0	0.0	5.6
N2	0.0	0.0	2.1	0.0	0.0	0.0	0.0	0.0	0.0	2.2
N3	0.0	0.0	0.7	0.1	0.0	0.0	0.0	0.0	0.0	0.8
N4	0.0	0.0	5.9	0.0	0.0	0.0	0.0	0.0	0.0	5.9
N5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
N6	0.0	0.0	4.6	0.0	0.0	0.0	0.0	0.0	0.0	4.7
S0	0.2	0.0	4.4	0.2	0.0	0.8	4.4	0.1	0.0	10.0
S1	0.1	0.0	19.3	0.1	0.5	0.3	2.9	0.0	115.0	138.2
S2	0.0	0.0	1.4	0.0	0.0	0.7	0.0	0.0	2.9	5.0
S3	6.2	10.5	55.6	22.4	12.3	22.2	98.4	2.3	1642.0	1871.9
S4	0.1	0.0	31.1	0.0	0.1	0.2	2.2	1.4	109.4	144.4
S5	0.4	0.0	23.6	0.0	1.6	0.3	51.8	0.0	426.1	503.8
S6	0.0	7.1	10.9	0.1	0.0	0.0	70.1	0.0	26.9	115.2

Appendix XIV. Bivalve biomasses (mg DM/m²) for each sampling site in Lake Saint-Pierre.

Site	DREI	SPHA	PISI	SPUM	SSPP	UNIO	ELLI	LAMP	LEPT	STRO	MOLL
N0	30.7	3.6	3.6	0.0	0.8	12123.3	11322.0	801.3	0.0	0.0	12183.7
N1	0.0	13.8	13.5	0.0	2.1	0.0	0.0	0.0	0.0	0.0	19.5
N2	0.0	32.4	32.2	2.4	2.8	0.0	0.0	0.0	0.0	0.0	34.5
N3	0.0	5.6	3.6	2.2	0.8	0.0	0.0	0.0	0.0	0.0	6.4
N4	0.0	12.5	12.5	1.2	3.3	2342.6	819.3	1523.3	0.0	0.0	2361.0
N5	0.0	16.0	16.0	0.1	1.7	0.0	0.0	0.0	0.0	0.0	16.0
N6	0.0	60.1	53.1	3.9	8.6	1496.5	273.1	1040.6	0.0	0.0	1561.3
S0	0.0	2.2	2.2	0.0	1.1	359.0	359.0	0.0	0.0	0.0	371.3
S1	106.1	6.2	5.1	1.1	1.6	3774.6	2573.8	1200.8	0.0	0.0	4025.1
S2	123.2	0.4	0.3	0.0	0.1	5113.7	2562.6	2551.1	0.0	0.0	5242.3
S3	27.5	12.2	4.4	7.8	1.5	55328.0	27106.7	26111.1	1007.3	61.8	57239.5
S4	0.0	3.5	2.8	0.0	0.6	11168.2	4541.8	6626.4	0.0	0.0	11316.1
S5	135.9	2.3	2.3	0.0	0.2	18204.9	9136.7	8702.3	0.0	0.0	18846.9
S6	0.0	5.5	5.5	0.0	1.9	14549.8	9363.8	5186.0	0.0	0.0	14670.5